A manual of physiology : for the use of junior students of medicine / by Gerald F. Yeo.

Contributors

Yeo, Gerald F. 1845-1909.

Publication/Creation

London : J. & A. Churchill, 1887 (London : Bradbury, Agnew.)

Persistent URL

https://wellcomecollection.org/works/q2y3j7hd

License and attribution

This work has been identified as being free of known restrictions under copyright law, including all related and neighbouring rights and is being made available under the Creative Commons, Public Domain Mark.

You can copy, modify, distribute and perform the work, even for commercial purposes, without asking permission.

wellcome collection

Wellcome Collection
183 Euston Road
London NW1 2BE UK
T +44 (0)20 7611 8722
E library@wellcomecollection.org
https://wellcomecollection.org

22101357517

A MANUAL

OF

PHYSIOLOGY

A MANUAL

OF

PHYSIOLOGY

FOR THE USE OF

JUNIOR STUDENTS OF MEDICINE

BY

GERALD F. YEO, M.D.DUBL., F.R.C.S.

PROFESSOR OF PHYSIOLOGY IN KING'S COLLEGE, LONDON, ETC.

SECOND EDITION

LONDON

J. & A. CHURCHILL

11, NEW BURLINGTON STREET

1887

2146
93188

WELLCOME INSTITUTE LIBRARY
Coll. welMOmec
Call No. QT4 1887 Y46m

M15332

PREFACE

TO THE SECOND EDITION.

In preparing this edition, I have done my utmost to correct inaccuracies and remove obscurities. The changes rendered necessary by recent research have also been made.

Some parts have been re-written ; notably the Chapters on the Central Nervous System, to which additional illustrations have been added.

The general arrangement remains the same as that of the First Edition.

I am again deeply indebted to my friend, Mr. E. F. Herroun, for much valuable assistance.

King's College, London,
August, 1887.

Digitized by the Internet Archive
in 2014

https://archive.org/details/b20392291

PREFACE

TO THE FIRST EDITION.

THE present volume has been written at the desire on the part of the Publishers that a new elementary treatise on Physiology should be added to the series of admirable students' manuals which they had previously issued.

In carrying this desire into execution I have endeavoured to avoid theories which have not borne the test of time, and such details of methods as are unnecessary for junior students. I do not give any history of how our knowledge has grown to its present standpoint; nor do I mention the names of the authorities upon whose writings my statements depend. I have also omitted the mention of exceptional points, because I find that exceptions are more easily remembered than the main facts from which they differ; and, since we must often be content with the retention of the one or the other, I have tried to ensure that it shall be the more important.

While endeavouring to save the student from doubtful and erroneous doctrines, I have taken great care not to omit any important facts that are necessary to his acquirement of as clear an idea as possible of the principles of Physiology.

I have not hesitated to lay unwonted stress upon those points which many years' practical experience as a teacher and an examiner has shown me are difficult to grasp and

are commonly misunderstood; and I have treated such subjects as are useful in the practice of medicine or surgery, more fully than those which are essential only to abstract physiological knowledge.

As medical students are generally obliged to commence the study of Physiology without any anatomical knowledge, I believe it to be absolutely necessary that their first physiological book should contain some account of the structure and relationships of the organs, the functions of which they are about to study. I have therefore added a short account of the construction of the various parts discussed in each chapter; it has, however, been found necessary to curtail this anatomical portion to a mere introductory sketch. Numerous illustrations, with full descriptions attached to each, are introduced to supplement the explanation given in the text.

So far as is consistent with an accurate treatment of the subject, I have avoided technical terms and scientific modes of expression. I know that in attempting to explain physiological truths in every-day language and in a plain common-sense way, I run the risk of appearing to lack the precision that such a subject demands; but after mature consideration, I have come to the conclusion that great scientific nicety and a scholastic style of expression have a deterrent effect upon the beginner's industry; and I think it better that he should acquire the first principles of the science in homely language, than pick up technical odds and ends in learned terms, the meaning of which he does not comprehend.

As many words, strange to the first year's student, have to be used, and must be learned, it has been thought advisable to add a short glossary, containing an explanation of the most ordinary physiological expressions.

Great difficulty is always found in fixing upon a starting point at which to begin the study of Physiology. To begin

with the circulation of the blood, which is so essential for the life of every tissue, one should have some knowledge of nerve and muscle. To begin with nerves and muscles, the mechanisms and the uses of the blood current should be understood; and so on, throughout the various systems, which are so inter-dependent that, for the thorough comprehension of any one, a knowledge of all is required.

I have, therefore, adopted the time-honoured plan of commencing with the vegetative systems and following the course of the aliments to their destination and final application, as I believe that this arrangement is open to as few objections as any other known to me.

I wish here to express my most cordial thanks to many friends who have aided me with kind assistance and advice. I am deeply indebted to Mr. W. Tyrrell Brooks for the great help he afforded me by compiling the chapters on Development; and I feel I cannot sufficiently thank Mr. E. F. Herroun for his untiring and valuable assistance in the revision of the proof sheets.

To Mr. G. Hanlon I am indebted for the careful and skilful manner in which he has executed the new woodcuts, most of which he had to copy from my rough drawings.

KING'S COLLEGE, LONDON,
January, 1884.

CONTENTS.

CHAPTER I.

The Objects of Physiology.

PAGE

Introductory Definitions 1
Structural and Physical Properties of Organisms 4
Chemical Composition 4
Vital Phenomena 6

CHAPTER II.

General View of the Structure of Animal Organisms.

Cells 8
Protoplasm, Nucleus, Cell-wall 10
Cell-contents 11
Varieties of Cells 12
Modifications of Original Cell-tissues 13
I. Epithelial Tissues 17
II. Nerve Tissues 20
III. Muscle or Contractile Tissues 23
IV. Connective Tissues 25

CHAPTER III.

Chemical Basis of the Body.

Elements in the Body 34
Classification of Ingredients found in the Tissues 36
Plasmata 36
Albuminous Bodies 38
Classification of Albumins 39
Albuminoids 42

CONTENTS.

CHAPTER I.

The Objects of Physiology.

PAGE

Introductory Definitions 1
Structural and Physical Properties of Organisms 4
Chemical Composition 4
Vital Phenomena 6

CHAPTER II.

General View of the Structure of Animal Organisms.

Cells 8
Protoplasm, Nucleus, Cell-wall 10
Cell-contents 11
Varieties of Cells 12
Modifications of Original Cell-tissues 13
I. Epithelial Tissues 17
II. Nerve Tissues 20
III. Muscle or Contractile Tissues 23
IV. Connective Tissues 25

CHAPTER III.

Chemical Basis of the Body.

Elements in the Body 34
Classification of Ingredients found in the Tissues 36
Plasmata 36
Albuminous Bodies 38
Classification of Albumins 39
Albuminoids 42

PAGE
Products of Tissue Change 43
Carbohydrates 47
Fats 48
Inorganic Bodies 49

CHAPTER IV.

The Vital Characters of Organisms.

Protoplasmic Movements 52
Reproduction 55
Bacteria 57
Amœba 59
Paramœcium 62

CHAPTER V.

Nutrition and Food Stuffs.

Classification of Foods 66
Composition of Special Forms of Food 69
Milk 69
Cheese, Meat, Eggs, &c. 72
Vegetables 73

CHAPTER VI.

The Mechanism of Digestion.

Mastication 78
Deglutition 79
Nervous Mechanism of Deglutition 84
Vomiting 86
Movements of the Intestines 88
Defæcation 90
Nervous Mechanism of the Intestinal Motion 92

CHAPTER VII.

Mouth Digestion.

Salivary and Mucous Glands 95
Characters of Mixed Saliva 98
Nervous Mechanism of Secretion of Saliva 100
Changes in the Gland-cells 107
Functions of the Saliva 109

CHAPTER VIII.

The Stomach Digestion.

PAGE
The Gastric Glands 111
The Characters of Gastric Juice 113
Mode of Secretion of Gastric Juice 114
Action of the Gastric Juice 116

CHAPTER IX.

Pancreatic Juice.

Structure of the Pancreas 122
Characters and Mode of Secretion of Pancreatic Juice 123
Changes in the Gland-cells 124
Action of Pancreatic Juice on Proteids 127
Action on Fats 128
Action on Starch 128

CHAPTER X.

Bile.

Functions of the Liver 129
Structure of the Liver 130
Composition and Method of obtaining Bile 135
Method of Secretion of Bile 138
Functions of the Bile 140

CHAPTER XI.

Functions of the Intestinal Mucous Membrane.

Structure of the Small Intestine 142
Method of obtaining Intestinal Secretion 144
Characters and Functions of the Intestinal Juice 145
Functions of the Large Intestine 147
Putrefactive Fermentations in the Intestine 148

CHAPTER XII.

Absorption.

Interstitial Absorption 149
The Lymphatic System 150

PAGE
Structure of Lymphatic Glands 153
Intestinal Absorption 157
Mechanism of Absorption 161
Materials Absorbed 163
Lymph and Chyle 165
Movement of the Lymph 168

CHAPTER XIII.

The Constitution of the Blood and the Blood-plasma.

General Characters of the Blood 171
Amount of Blood in the Body 172
Physical Construction of the Blood, Blood-plasma 174
Preparation and Properties of Fibrin 175
Chemical Composition of Plasma 176
Serum 179

CHAPTER XIV.

Blood Corpuscles.

Proportion of Red to White 180
White Blood-cells 181
Origin of the Colourless Blood-cells. 183
The Red Corpuscles, Sizes and Shapes 184
Action of Reagents on Red Corpuscles 186
Method of counting Corpuscles 188
Chemistry of the Colouring Matter of the Blood 190
Spectra of Hæmoglobin 192
Hæmatin, Hæmin, &c. 194
Development of the Red Disks 196
The Gases of the Blood 197

CHAPTER XV.

Coagulation of the Blood.

Formation of the Blood-clot 199
Circumstances influencing Coagulation 201
The Cause of Coagulation 202
Coagulation in the Vessels 203
Formation of Fibrin 205

CHAPTER XVI.

The Heart.

PAGE
Pulmonary and Systemic Circulations 208
Method of the Circulation of the Blood 209
The Heart 211
Arrangement of Muscle Fibre 213
Minute Structure of the Heart 214
Action of the Valves 216
Cycle of the Heart-beat 218
Movements of the Heart 220
The Heart's Impulse 221
Heart-sounds 223
Innervation of the Heart 225
Local Centres 226
Inhibitory Nerves 230
Accelerator Nerves 231
Afferent Cardiac Nerves 232

CHAPTER XVII.

The Blood-vessels.

Structure of the Vessels 233
The Capillaries 235
Relative Capacity of the Vessels 237
Physical Forces of the Circulation 239
The Blood-pressure 240
Measurement of Blood-pressure 244
Variations in the Blood-pressure 248
Influence of Respiration on the Blood-pressure 249
The Arterial Pulse 254
Methods of obtaining Pulse-tracings 256
Variations in the Pulse 258
Velocity of the Blood-current 259
Controlling Mechanisms of the Blood-vessels 263

CHAPTER XVIII.

The Mechanism of Respiration.

Gas Interchange 268
Structure of the Lungs and Air-passages 270
The Thorax 273
Thoracic Movements 275

PAGE
Inspiratory Muscles 277
Expiration 281
Function of the Pleura 282
Pressure Differences in the Air 284
The Volume of Air 284
Nervous Mechanism of Respiration 286
Modified Respiratory Movements 291

CHAPTER XIX.

The Chemistry of Respiration.

Composition of the Atmosphere 293
Expired Air 294
Changes the Blood undergoes in the Lungs . . . . . 29(
Gases in the Blood 29
Internal Respiration 300
Respiration of Poisonous Gases 301
Ventilation 302
Asphyxia 303

CHAPTER XX.

Blood-elaborating Glands.

Ductless Glands 9
Supra-renal Capsule and Thyroid Body . . . . . .
Thymus . . . . . 3(
Spleen 309
Functions of the Spleen 311
Glycogenic Function of the Liver 313
Glycogen . . . . . 31.

CHAPTER XXI.

Secretions.

Lachrymal Glands 318
Mucous Glands . . . . . .
Sebaceous Glands . . . . . .
Mammary Glands 3
Composition of Milk . . . . . 3.
Sudoriferous Glands . . . . . 32(
Cutaneous desquamation 328

CHAPTER XXII.

Urinary Excretion.

PAGE
Structure of the Kidneys 330
Blood-vessels of the Kidneys 332
Urine 334
Method of Secretion of the Urine 335
Chemical Composition of Urine 338
Urea 339
Uric Acid 340
Kreatinin, Xanthin, Hippuric Acid, Oxalic Acid, &c. 341
Colouring Matters and Inorganic Salts 342
Abnormal Constituents 343
Urinary Calculi 344
Source of Urea, &c. 345
Nervous Mechanism of the Urinary Secretion 347
Outflow of Urine 349
Nervous Mechanism of Micturition 351

CHAPTER XXIII.

Nutrition.

Changes during Starvation 353
Requirements 356
The Uses of Food Stuffs 359

CHAPTER XXIV.

Animal Heat.

Warm and Cold-blooded Animals 363
Variations in the Body Temperature 364
Mode of Production of Animal Heat 366
Income and Expenditure of Heat 367
Maintenance of Uniform Temperature 369

CHAPTER XXV.

Contractile Tissues.

Physiology of Muscle 376
Properties of Muscle in the Passive State 378
Electric Phenomena of Muscle 381

PAGE
Active State of Muscle 384
Muscle Stimuli 385
Changes occurring in Muscle on its entering the Active State . . 387
Muscle Contraction 388
Graphic Method of Recording Contraction 392
Tetanus, Fatigue, &c. 398
Rigor Mortis 403
Unstriated Muscle 405

CHAPTER XXVI.

The Application of Skeletal Muscles.

General Arrangements 407
Joints 408
Standing 410
Walking and Running 413

CHAPTER XXVII.

Voice and Speech.

Anatomical Sketch 415
Mechanism of Vocalisation - 417
Properties of the Human Voice 420
Nervous Mechanism of Voice 421
Speech 422

CHAPTER XXVIII.

General Physiology of the Nervous System.

Anatomical Sketch 424
Functional Classification 426
Chemistry and Electric Properties of Nerves 427
The Active State of Nerve-fibres 428
Nerve Stimuli 429
Velocity of Nerve-impulse 431
The Electric Changes in Nerves 433
Electrotonus 433
Irritability of Nerve Fibres 435
Law of Contraction 438
Nerve Corpuscles and Terminals 439
Functions of the Nerve Cells 441

CHAPTER XXIX.

Special Physiology of Nerves.

PAGE
Spinal Nerves 445
The Cranial Nerves 448
The Trochlear Nerve, Portio Dura, &c. 449
Efferent and Afferent Fibres 451
Ganglia of the Fifth Nerve 453
The Glosso-pharyngeal Nerve 454
The Vagus Nerve 455
The Hypoglossal Nerve 457

CHAPTER XXX.

Special Senses.

Skin Sensations 460
Nerve Endings 461
Sense of Locality 464
Sense of Pressure 466
Temperature Sense 481
General Sensations 469

CHAPTER XXXI.

Taste and Smell.

Sense of Taste 472
Sense of Smell 475

CHAPTER XXXII.

Vision.

The Construction of the Eye-ball 478
Dioptric Media of the Eye-ball 481
Structure of the Lens 482
The Dioptrics of the Eye 485
Accommodation 490
Defects of Accommodation 492
Defects of Dioptric Apparatus 493
The Iris 495
The Ophthalmoscope 498
Visual Impressions 501

PAGE
The Function of the Retina 502
Colour Perceptions 509
Mental Operations in Vision 512
Movements of the Eye-balls 512
Binocular Vision 514

CHAPTER XXXIII.

Hearing.

Sound 516
Conduction of Sound-vibrations through the Outer Ear . . . 519
Conduction through the Tympanum 520
Conduction through the Labyrinth 524
Stimulation of the Auditory Nerve 527

CHAPTER XXXIV.

Central Nervous Organs.

Nerve Cells 530
The Spinal Cord as a Conductor 532
The Spinal Cord as a Collection of Nerve Centres 540
Special Reflex Centres 547
Automatism 549

CHAPTER XXXV.

The Medulla Oblongata.

The Medulla Oblongata as a Conductor 551
The Respiratory Centre 554
The Vaso-motor Centre 555
The Cardiac Centre 557

CHAPTER XXXVI.

The Brain.

The Mesencephalon and Cerebellum 561
Crura Cerebri 564
Basal Ganglia 565
Cerebral Hemispheres 568
Localisation of the Cerebral Functions 571

CHAPTER XXXVII.

Reproduction.

PAGE
Origin of Male and Female Generative Elements 577
Menstruation and Ovulation 580
Changes in the Ovum subsequent to Impregnation 582
Formation of the Membranes 586
The Placenta 592

CHAPTER XXXVIII.

Development.

Development of the Vertebral Axis 597
Development of the Central Nervous System 602
The Alimentary Canal and its Appendages 608
The Genito-urinary Apparatus 612
The Blood-vascular System 619
Development of the Eye 631
Development of the Ear 635
Development of the Skull and Face 638

Glossary 643

INDEX 653

COMPARISON OF THE METRICAL WITH THE COMMON MEASURES.

By Dr. Warren De la Rue.

MEASURES OF LENGTH.

	In English Inches.	In English Feet = 12 Inches.	In English Yards = 3 Feet.	In English Fathoms = 6 Feet.	In English Miles = 1,760 Yards.
Millimeter	0·03937	0·0032809	0·0010936	0·0005468	0·0000006
Centimeter	0·39371	0·0328090	0·0109363	0·0054682	0·0000062
Decimeter	3·93708	0·3280899	0·1093633	0·0546816	0·0000621
Meter	39.37079	3·2808992	1·0936331	0·5468165	0·0006214
Decameter	393·70790	32·8089920	10·9363310	5·4681655	0·0062138
Hectometer	3973·07900	328·0899200	109·3633100	54·6816550	0·0621382
Kilometer	39370·79000	3280·8992000	1093·6331000	546·8165500	0·6213824
Myriometer	393707·90000	32808·9920000	10936·3310000	5468·1655000	6·2138244

1 Inch = 2·539954 Centimeters. | 1 Foot = 3·0479449 Decimeters. | 1 Yard = 0·91438348 Meter. | 1 Mile = 1·6093149 Kilometers.

MEASURES OF CAPACITY.

	In Cubic Inches.	In Cubic Feet = 1,728 Cubic Inches.	In Pints = 34·65923 Cubic Inches.	In Gallons = 8 Pints = 277·27384 Cubic Inches.	In Bushels = 8 Gallons = 2218·19075 Cubic Inches.
Milliliter or cubic centimeter	0·061027	0·0000353	0·001761	0·00022010	0·000027512
Centiliter or 10 cubic centimeters	0·610271	0·0003532	0·017608	0·00220097	0·000275121
Deciliter or 100 cubic centimeters	6·102705	0·0035317	0·176077	0·02200967	0·002751208
Liter or cubic decimeter	61·027052	0·0353166	1·760773	0·22009668	0·027512085
Decaliter or centistere	610·270515	0·3531658	17·607734	2·20096677	0·275120846
Hectoliter or decistere	6102·705152	3·5316581	176·077341	22·00966767	2·751208459
Kiloliter or stere, or cubic meter	61027·051519	35·3165807	1760·773414	220·09667675	27·512084594
Myrioliter or decastere	610270·515194	353·1658074	17607·734140	2200·96676750	275·120845937

1 Cubic Inch = 16·3861759 Cubic Centimeters. | 1 Cubic Foot = 28·3153119 Cubic Decimeters. | 1 Gallon = 4·543457969 Liters.

MEASURES OF WEIGHT,

	In English Grains.	In Troy Ounces = 480 Grains.	In Avoirdupois Lbs. = 7,000 Grains.	In Cwts. = 112 Lbs. = 784,000 Grains.	Tons = 20 Cwt. = 15,620,000 Grains.
Milligram	0·015432	0·000032	0·0000022	0·00000002	0·000000001
Centigram	0·154323	0·000322	0·0000220	0·00000020	0·000000010
Decigram	1·543235	0·003215	0·0002205	0·00000197	0·000000098
Gram	15·432349	0·032151	0·0022046	0·00001968	0·000000984
Decagram	154·323488	0·321507	0·0220462	0·00019684	0·000009842
Hectogram	1543·23480	3·215073	0·2204621	0·00196841	0·000098421
Kilogram	15432·34800	32·150727	2·2046213	0·01968412	0·000984206
Myriogram	154323·48000	321·507267	22·0462126	0·19684118	0·009842059

CORRESPONDING DEGREES IN THE FAHRENHEIT AND CENTIGRADE SCALES.

Fahr.	Cent.	Cent.	Fahr.
500°	260°·0	100°	212°·0
450°	232°·2	98°	208°·4
400°	204°·4	96°	204°·8
350°	176°·7	94°	201°·2
300°	148°·9	92°	197°·6
212°	100°·0	90°	194°·0
210°	98°·9	88°	190°·4
205°	96°·1	86°	186°·8
200°	93°·3	84°	183°·2
195°	90°·5	82°	179°·6
190°	87°·8	80°	176°·0
185°	85°·0	78°	172°·4
180°	82°·2	76°	168°·8
175°	79°·4	74°	165°·2
170°	76°·7	72°	161°·6
165°	73°·9	70°	158°·0
160°	71°·1	68°	154°·4
155°	68°·3	66°	150°·8
150°	65°·5	64°	147°·2
145°	62°·8	62°	143°·6
140°	60°·0	60°	140°·0
135°	57°·2	58°	136°·4
130°	54°·4	56°	132°·8
125°	51°·7	54°	129°·2
120°	48°·9	52°	125°·6
115°	46°·1	50°	122°·0
110°	43°·3	48°	118°·4
105°	40°·5	46°	114°·8
100°	37°·8	44°	111°·2
95°	35°·0	42°	107°·6
90°	32°·2	40°	104°·0
85°	29°·4	38°	100°·4
80°	26°·7	36°	96°·8
75°	23°·9	34°	93°·2
70°	21°·1	32°	89°·6
65°	18°·3	30°	86°·0
60°	15°·5	28°	82°·4
55°	12°·8	26°	78°·8
50°	10°·0	24°	75°·2
45°	7°·2	22°	71°·6
40°	4°·4	20°	68°·0
35°	1°·7	18°	64°·4
32°	0°·0	16°	60°·8
30°	— 1°·1	14°	57°·2
25°	— 3°·9	12°	53°·6
20°	— 6°·7	10°	50°·0
15°	— 9°·4	8°	46°·4
10°	—12°·2	6°	42°·8
5°	—15° 0	4°	39°·2
0°	—17°·8	2°	35°·6
— 5°	—20°·5	0°	32°·0
—10°	—23°·3	— 2°	28°·4
—15°	—26°·1	— 4°	24°·8
—20°	—28°·9	— 6°	21°·2
—25°	—31°·7	— 8°	17°·6
—30°	—34°·4	—10°	14°·0
—35°	—37°·2	—12°	10°·4
—40°	—40°·0	—14°	6°·8
—45°	—42°·8	—16°	3°·2
—50°	—45°·6	—18°	—0°·4
		—20°	—4°·0

MANUAL OF PHYSIOLOGY.

CHAPTER I.

THE OBJECTS OF PHYSIOLOGY.

Biology, the science which deals with living beings, may be divided into two branches, viz. :—

1. Morphology, which treats of the forms and structure of living creatures ; and,

2. Physiology, which attempts to explain the modes of activity exhibited by them during their life-time, and may therefore be defined as the science which investigates the phenomena presented by the textures and organs of healthy living beings ; or, in short, the study of the actions of organisms in contradistinction to that of their shape and structure.

The organic or living world is naturally divided into the Animal and Vegetable kingdoms. We have, therefore, both animal and vegetable morphology and physiology. In studying the vegetable kingdom, the form and structure, as well as the activity of plants are associated together to form the subject known as Botany. The physiology of plants need not, therefore, be considered here ; though, indeed, a knowledge of it proves useful in considering many of the processes belonging to animal life. On the other hand, the morphology and the physiology of animals are commonly taught separately, and in the medical curriculum are made distinct subjects.

Morphology includes the external form, the general construction or anatomy of organisms, and the minute structure of their textures as revealed by the microscope. This latter branch of study, under the name Histology, has now developed into a very extensive subject, which is inseparable from either physiology or anatomy. In this country histology is commonly taught in the medical schools

with physiology, because the time of the teachers of morphology is occupied in expounding the nomenclature of descriptive anatomy, while the microscope is in everyday use in the physiological laboratory. Moreover, an adequate knowledge of microscopic methods, and of the various form-elements of the different textures of the body is one of the first essentials for physiological study.

As the different actions of the body are performed by different tissues, which in the higher animals are grouped together as distinct organs, a general idea of the position and construction of these different parts of the body must be acquired before the study of physiology can be commenced. Anatomy and general morphology are the frameworks upon which physiological knowledge is built up. Some knowledge of these subjects must therefore precede the study of physiology, in order that the student may be in a position to grasp even the simplest facts connected with any physiological question.

We shall soon find that the assistance of other sciences is also indispensable to physiology. Thus every action of a living texture or tissue is accompanied by some chemical change, the chemical process in fact being the common essential part of the phenomena of life. The student of physiology must, then, know something of the science of chemistry ; indeed the mode of action of chemical elements forms quite as important a groundwork for the study of the activity of the living tissues as their general form or minute structure.

Further, the laws which govern the motions of inanimate bodies also control the actions of living tissues, for we cannot claim to understand or recognise the existence of any laws affecting living organisms other than those known to be applicable to dead matter. There are a great number of activities shown by living textures which we cannot explain by the recognised laws of chemistry or physics. We therefore use, for convenience sake, the term "vital phenomena," to indicate processes which are beyond our present chemical and physical knowledge. In using this term we must not think it implies a separate set of natural laws belonging to life. We cannot discover or formulate any special laws affecting living beings only, and therefore we must not assume that any such exist. We must rather endeavour to explain all the so-called "vital phenomena" by means of the laws known to chemists and physicists. By this means we shall certainly get a closer insight into the processes of life, and if there be laws governing the living beings we may learn to know them. This method of working has already given good results, for within comparatively recent times many of the processes which were

regarded as specially vital in character have been shown to be within the power of the experimenter and to depend on purely physico-chemical processes.

It is therefore necessary for the physiologist, before he attempts to explain the activities of any organism, to be familiar not only with the structure of its body, but also with the various laws which chemists and physicists teach us control the operations of inanimate matter.

The sciences of chemistry and physics may, in fact, be regarded as the physiology of inorganic matter, just as when chemistry and physics are applied to the elucidations of the functions of living creatures by the biologist, the study is called physiology. When we consider how far from thoroughly grasping and interpreting all the phenomena presented by the various kinds and conditions of matter the chemist and the physicist still are, we cannot be surprised that those who attempt to explain the actions of living beings find many processes that they are unable to comprehend. So that when physiologists make use of the convenient term "vital phenomena," it must be remembered that they do not thereby imply the existence of a special living force or any kind of energy peculiar to living creatures.

The ultimate object of physiology is not yet within the reach of our modern methods of research. To explain the mode of activity of living beings, and grasp the exact relation borne by their living phenomena to the laws which govern them, is a task of enormous difficulty. Indeed the manifestations of certain energies in living organisms are so complicated that it is often, if not generally, impossible to say exactly how they are brought about, and we are therefore obliged, for the present at least, to be satisfied with the mere recognition and description of the phenomena.

Since the human organism is the special study of students of medicine, the contents of this volume should properly be restricted to the physiology of man. But human physiology cannot be studied alone; because in man we cannot watch sufficiently closely, or question fully, by experiment, the phenomena of life. Further, no sharp line of separation can be drawn between the actions of the various organs of man and those of the lower animals. The consideration of the physiology of those animals which are akin to man must therefore go hand in hand with the study of the physiology of man himself. Much light has been thrown on the actions of the complex textures of the highest animals, by the observation of the activities of the lowest organisms, where the manifestations of life may be carefully watched with the microscope in the living animal under its normal conditions.

GENERAL CHARACTERS OF ORGANISMS.

The term organism, which is commonly used as having the same meaning as *living being*, owes its derivation to the complexity of structure common among the higher forms of life, which are made up of several distinct organs. This organic construction does not hold good as a distinguishing mark between living beings and inanimate matter, because we are acquainted with a vast number of living organisms, both plants and animals, which are not made up of organs, but are composed of a minute piece of a soft jelly-like material, which is simply granular throughout, and devoid of structural differentiation during the life of the creature.

We may classify the general characters of living beings as follows :

1. Structural and physical properties.
2. Chemical composition.
3. Activities during life (vital phenomena).

1. Structural Characters of Organisms.—The minute structure of living beings as shown by the microscope no doubt helps to distinguish the textures of organisms from inorganic structures. Although organic textures are found to differ very widely in their characters they are all related in one respect, namely, that at the earliest period of their existence they consist of a minute mass of a substance called *Protoplasm*, known as a *cell*. In plants a cellular structure remains obvious in all parts of the adult, no matter how much the texture may be modified by adaptation to the requirements of any given duty or function. If we examine with the microscope the leaves, bark, wood, or pith of a plant, in all of them a cellular structure can be recognised. In the less developed members of the animal kingdom, and during the initial stages in the existence of the highest animals, the textures are composed exclusively of aggregations of living cell-elements. We shall shortly see that in the more fully developed condition of the higher animals, the cells become variously modified in form and function, and the protoplasm manufactures various structures adapted to the performance of the diverse functions of the different parts. In all organic textures which can be said to be living, cells are dispersed in greater or less number, and regulate their nutrition and repair.

2. Chemical Composition.—There are no characters in the chemical composition of the textures of organic beings which can be

said to be absolutely distinctive or to separate them from inorganic matter. No doubt their chemical construction frequently exhibits certain peculiarities, not seen in dead matter, which may be taken as characteristic, but living textures only differ in the general plan of arrangement and composition from that most commonly met with in the construction of inorganic materials.

In the first place, the great majority of the *chemical elements* which we know of, take no share in the formation of living creatures, and are never found to enter into their composition. Practically only fifteen of some seventy *elements* known to chemists take part in making up the tissues of animals. The majority of these are only present in very small quantity and with no great constancy. On the other hand, there are four elements, namely, *carbon*, *oxygen*, *hydrogen*, and *nitrogen*, which are found with such great regularity and in so great quantity, that they may be said to make up the great bulk (97 per cent.) of the animal frame. The great constancy with which the first three of these elements occur must be regarded as a most important character of organic tissues.

Secondly, in *organic substances* the chemical elements are associated in much more complex and irregular proportions. Generally a large number of *atoms*, of each element, are grouped together to form the *molecule*, and often the compound is so complex that its chemical formula remains a matter of doubt. As an example of the complexity of bodies found in organic analysis, a remarkable substance called *lecithin*, which appears in the analysis of protoplasm and many tissues, may be mentioned. Its formula may be expressed thus :

$$C_3 H_5 \begin{cases} C_{18} H_{35} O_2 \\ C_{18} H_{35} O_2 \\ O - PO \begin{cases} O H N (C H_3)_3 \\ O - C_2 H_4 - O H. \end{cases} \end{cases}$$

It is peculiar in containing nitrogen and phosphorus, and in construction is said to be like a fat.

In *inorganic substances*, on the other hand, the elements are found to be combined, as a general rule, in simple and regular proportions. The molecules are made up of but few elements arranged in a definite manner and firmly bound together, so that they are not prone to undergo decomposition. As an example, we may take water, which has the well-known formula,

$$H_2O.$$

Though these bodies may be taken as types of organic and inorganic substances respectively, it must not be imagined that all organic bodies are as complex, irregular, and unstable as lecithin, or that inorganic compounds, as a rule, are invariably simple and stable like water.

It is further remarkable that *Carbon*—an element which is exceptional in forming but few associations in the mineral world, where it chiefly combines with oxygen to form CO_2—is almost invariably present in living textures, in which it is combined with hydrogen and nitrogen as well as oxygen in various proportions. The constancy of carbon as an ingredient of organic bodies is so great that what formerly was called organic chemistry is now often called the chemistry of the carbon compounds.

These complex associations of many atoms of carbon with many atoms of other elements, are readily dissociated when exposed to the air under even slightly disturbing influences. When heated to a certain degree they burn, *i.e.*, unite rapidly with the oxygen of the air; and in the presence of minute organisms they putrefy. Thus *instability* is a general feature commonly met with in most substances of organic origin.

Chemical instability reaches the highest pitch in tissues which are actually alive and engaged in vital processes. So long as any texture lives, *i.e.*, is capable of performing its functions, it must constantly undergo certain chemical changes, a kind of decomposition, tending to produce disintegration, and a re-integration by means of new chemical associations with fresh materials. A tissue may then be said to deserve the term living, only as long as it undergoes these antagonistic chemical changes. The tendency to destructive oxidation or disintegration is intimately connected with the functional activity of the living texture and increases with this activity. The re-integration or constructive process requires the presence of suitable materials with which the texture may combine, in order to make up for the loss. Thus living tissues are ever on the point of destruction, which can only be warded off by the timely reconstruction of their chemical ingredients by suitable fresh materials. This reconstruction by means of fresh matter from without is called *assimilation*, and forms the most, if not the only, satisfactory criterion by which adequately to distinguish living beings from inorganic matters.

The object of assimilation is to supply suitable fresh materials to the various textures for the chemical processes required for their function while living. This will be found to form a great part of

physiological study. Further, the energy manifested in the living activity of the textures depends upon the various oxidising processes, and the exact laws which govern these combustions, and the results they produce in the various tissues, practically make up the other part of physiology.

3. VITAL PHENOMENA.—The so-called vital phenomena which take place in the textures of organisms are, for the most part, performed by the agency of the living cell-elements, in which we can recognise independent manifestations of life, such as the response to stimuli, motion, nutrition, growth, &c. The living activity of organisms requires for its perfect development certain external conditions, namely, a certain degree of *warmth* and *moisture*. Without a certain degree of warmth and moisture the chemical interchanges just mentioned cannot go on, and the organism is either destroyed or remains in a state of inactivity.

The nutrition of the animal body which is accomplished by means of the processes of assimilation already mentioned enables it to grow, and, up to a certain point, increase in size, and further undergo many changes in form and texture. There is, however, a limit to this assimilative power: nutritive activity diminishes, growth gradually stops, and after a time decay appears and is followed by death.

Thus organisms exist only for a limited period of time, during which their size, form, and functional activity are constantly undergoing some general alteration dependent on or concurrent with the incessant changes in their molecular construction.

This cycle of changes through which organisms pass we speak of as their life-time. During this life-time, at the period when their functional activity is at its height, they possess the remarkable faculty of producing individuals like themselves.

This is accomplished by setting apart a cell which, under favourable circumstances, assumes special powers of growth, increases in size by the rapid formation of new cells, and developes into an independent living unit. In time it arrives at maturity, and becomes like its parent, and then passes through the same cycle—by its power of assimilation it grows to maturity, reproduces its like, decays, and dies.

CHAPTER II.

GENERAL VIEW OF THE STRUCTURAL CHARACTERS OF ANIMAL ORGANISMS.

THE parts played by *Cells* in the functions of living beings are so many and so important that it is necessary at the very outset to consider the properties of the individual elements somewhat in detail.

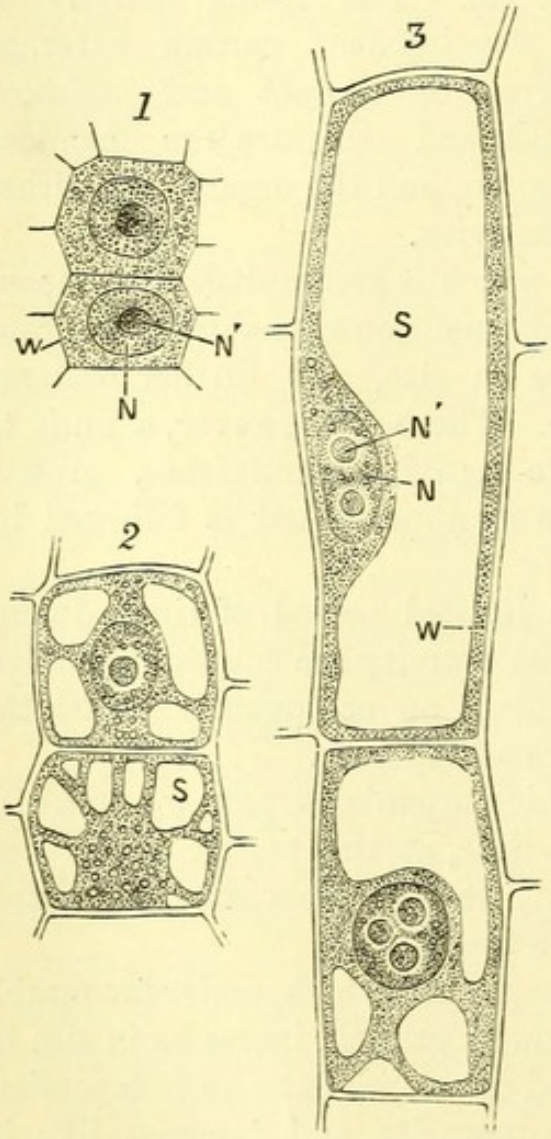


Fig. 1.—Cells from the root of a plant. (×550.)

1. Showing youngest cells with thin walls (w) filled with protoplasm and containing nucleus (n), and nucleolus (n').
2. Older cells with thicker walls with vacuoles and cell-sap (s).
3. Shows further diminution of protoplasm and increase in cavity (s) in proportion to the growth of the cell wall (w).

The demonstration of the cellular structure of plants was first made in 1832 by a distinguished German botanist named Schlieden, who considered the cells to be characteristic of plant tissue. A few years later Schwann showed that the animal tissues, though not so obviously, were also made up of cells, and that they owed their beginning and development to the activity of cell elements. Thus originated the "cellular theory," which, with some modifications, is now the basis of all physiological enquiry.

The first idea which was conveyed by the term *cell* varied much from that which we now accept as a proper definition of such an organic unit.

Fully developed vegetable cells being the first discovered were taken as the type of all. The main characteristics of these may be briefly summed up. First, a membranous sac called the *cell-*

wall, generally very well defined, and, secondly, within the cell-wall various *cell-contents*. Among the more conspicuous of the latter may be mentioned (1) a soft, clear, jelly-like substance called protoplasm, in which lies a nucleus, and (2) certain cavities called vacuoles, which are filled with a clear fluid or cell-sap.

Further investigation of the life history of cells, particularly in the early stages of their development, showed that the cell-wall, which played so important a part in the original conception of a cell was not always present, but was formed by the protoplasm in a later stage of growth. The cell-sap and other matters were found to occur less commonly, and appeared still later than the cell-wall in the life-time of the vegetable cell; hence it was concluded that they

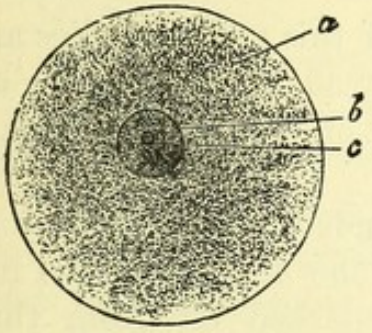


Fig. 2.—Diagram of animal cell (ovum). (Gegenbauer.)
a. Granular protoplasm.
b. Nucleus.
c. Nucleolus.

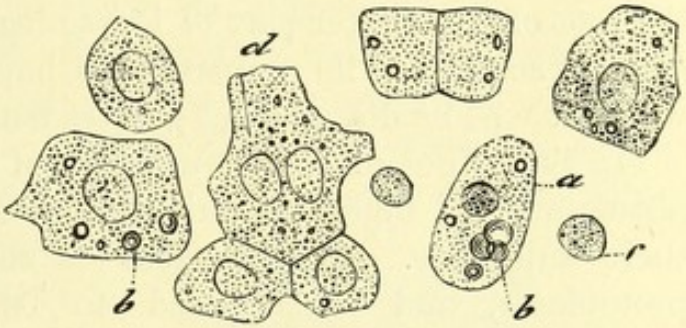


Fig. 3.—Liver cell of man, containing fat globules (*b*) and biliary matters. (Cadiat.)

were the outcome of changes due to the activity of the protoplasm, and that this latter was the only essential and formative part of the cell.

Subsequently, from the facts that some vegetable cells in the youngest and most active stage of their growth have no limiting wall, and that most animal cells have none during any part of their life, it was proposed to define a cell as *a mass of protoplasm containing a nucleus*. But further research showed that the nucleus was not always present. In many cryptogamic plants no nucleus can be found, and in some animal cells, which must be regarded as independent individuals (Protamœba), there is no nucleus at any part of their life-time. This would lead us to suppose that *a mass of protoplasm capable of manifesting all the phenomena of life* would be a sufficient definition. Though this is probably correct in a few cases, the vast majority of cells do contain nuclei. As it is difficult to divest our minds of the connexion between the two, it has been proposed to give the name *cytode* to the non-nucleated forms, which certainly are very exceptional, reserving the term *cell* for the common nucleated unit.

Each part of the cell may now be considered in the order of its importance, viz., protoplasm, nucleus, cell-wall, and cell-contents.

I. PROTOPLASM is commonly seen to be a colourless, pale, milky, semi-translucent substance, more or less altered in appearance by various foreign matters lying in it. These latter also give it a granular appearance, and when dead it commonly exhibits a linear marking or fine network. During life its consistence is nearly fluid, varying with the circumstances in which it is placed, from that of a gum solution to a soft jelly. When living unmolested in its normal medium it seems to flow into various shapes, but this is a living action which does not prove it to be diffluent, for any attempt to investigate it by experiment causes a change in its consistence approaching to rigidity.

As the full comprehension of the function of this substance lies at the root of the greater part of Physiology, the reader is referred for a detailed account of its properties to Chapter III. on Vital Phenomena, where it will be discussed at greater length.

II. THE NUCLEUS.—The majority of independent masses of protoplasm, and all highly organized cells, contain one or more nuclei in their substance. The nucleus is sharply marked off from the protoplasm, and is supposed to be surrounded by a special limiting membrane. Its presence can generally be made much more conspicuous by treating the cell with certain chemical re-agents, notably dilute acids and various dyes. The nucleus is able to resist the action of dilute acetic acid better than the remainder of the cell, so that it stands out clearly, when the rest becomes transparent. Many staining agents such as magenta (one of the aniline dyes) colour the nucleus more quickly and deeply than the protoplasm. Although it is accredited with special independent movements that occur under certain circumstances, compared with the protoplasm it is not very contractile. It appears to be intimately associated with the vital phenomena of the cell, and may be said to control or initiate its most important activity, namely, its division. In the *nuclear matrix*, which is clear and homogeneous, may often be seen an irregular network, one point of which stands out more clearly, and is called the nucleolus. Remarkable changes in the arrangement of this network are seen in some cells to precede the division of the protoplasm. This is called *karyokinesis*.

III. THE CELL-WALL.—It has already been stated that the most active cells, such as are found in the earliest stages in the life of an organism (embryonic cells), have no enclosing membrane or cell-wall. But in the more advanced stages of cell life we find this

second form of protoplasmic differentiation to be common enough. In animal cells the limiting membrane has never the same importance as the cell-wall in vegetable tissues, where some of the principal textures may be traced to a direct modification of the cell-wall, still recognizable as such. Whenever such a limiting membrane exists, it is formed by the outer layers of protoplasm undergoing changes so as to become of greater consistence. In the animal tissues the cells form various structures, which are not limiting membranes or cell-walls, but rather give the idea of lying between the cells. Hence, in one large group of tissues, they have been called *intercellular substance*, while in others they appear as materials specially modified for the furtherance of the functions of the special tissues.

IV. Cell-Contents.—Regarding protoplasm as the essential living part of the cell, under this heading will come only those extraneous matters which are the outcome of protoplasmic activity.

The cell-contents which are present with such constancy and in such variety in vegetable cells, form in them an all-important part; but in most animal cells the contents do not occupy such a striking position.

No doubt animal protoplasm is quite as capable as that of vegetables of making out of its own substance, or the nutriment supplied to it, a great variety of materials, but these are seldom stored in such large quantities in animal cells as in those of plants.

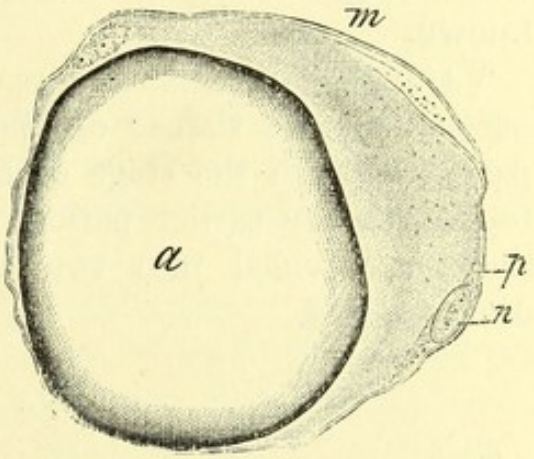


Fig. 4.—Cell from connective tissue containing large fat globule (*a*), and showing protoplasm (*p*), and nucleus (*n*), (*m*) membrane. (Ranvier.)

In the cells of some kinds of animal textures, particularly that called *Connective Tissue*, we commonly find large quantities of fat formed and accumulated to such a degree in the cell that the protoplasm can be no longer recognized as such. Its remnant is devoted to forming a limiting membrane for the fatty contents, so that the cell is converted into an oil vesicle, and here what may be termed the contents become the most important part of the cell. In various glandular cells as will be seen hereafter, different substances are made and stored up temporarily in the protoplasm. These may be seen as bright

refracting granules, which are subsequently discharged in the secretion of the gland.

In other cells (liver) nutrient material allied to starch may be deposited in considerable quantity, just as starch is stored in certain cells of plants, but owing to the greater and more constant activity of animals, the amount laid by never attains anything like that found in the store-textures of vegetables, where the result of an entire summer's active work is put by as a provision for the next winter and the fresh burst of energy which follows it in the spring.

But while the above are all more or less temporary contents of cells, we have an example of a permanent deposit in them, viz., pigment, this substance is formed by the protoplasm in various parts, and has a special physiological use. Thus in the tissue behind the retina—or nerve layer of the eye-ball—the cells are filled with granules of a pigmented substance, which absorbs the light falling upon it, and thus prevents the reflections which would interfere with the clearness of sight.

It also occurs in the skin of the negro and other races, and in that of the frog and other animals, but in these its function is not fully known.

VARIETIES OF CELLS.—Great varieties of cells are found in the various mature tissues of the higher animals, all of which have passed through the stage of being a simple nucleated mass of protoplasm in the earlier periods of their development. All cells may then be divided into two chief types, the indifferent and the differentiated.

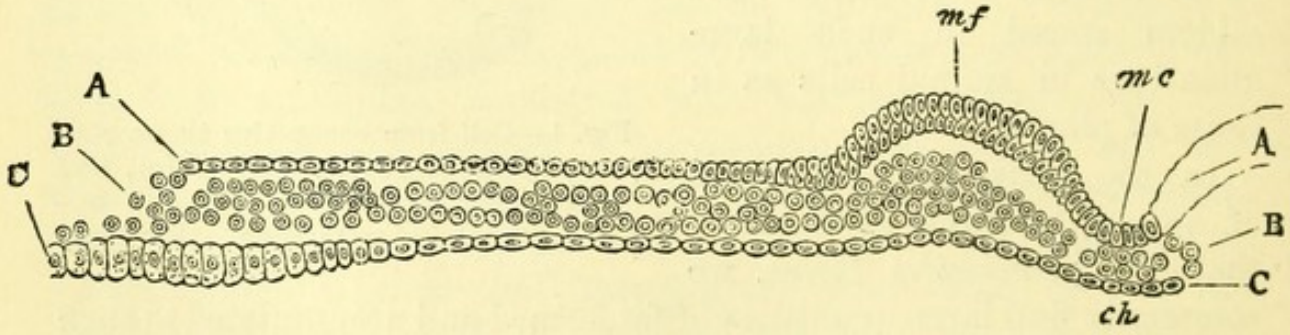


Fig. 5.—Transverse section of Blastoderm, showing the elements in the earlier stage of the development. A, epiblast; B, mesoblast; C, hypoblast.

Under the category of *indifferent cells* may be placed all such as retain the characters of the first embryonic cells, and have not acquired any special structure or property by which they can be distinguished from the simplest form. Such cells are the only ones

in the early stages of the embryo. In the adult tissues they also occur, having various duties to perform. They are found in the blood and lymph, and scattered throughout the tissues. They are without a cell-wall, and have no special contents to mark their function.

Among the *differentiated cells* we find many special characters, adapting them to certain special duties, for all these cells are modified from the original type and applied to the performance of some special function.

Space prevents even a short enumeration of the varieties of cells met with in the tissues of plants, where they not only carry on the active functions of the organism, but also form the supporting structures.

The differentiation of a cell is accomplished by its protoplasm, which forms new structural parts, and itself sometimes seems to diminish in quantity until an element is produced in which there may be no protoplasm recognizable.

We find then matured and differentiated cells which vary—

1. In shape, being spherical, flattened, fusiform, stellate, &c.
2. In size.
3. In their mode of connection.

Cells may also be classified according to their function, *e.g.*, Glandular, Nervous, &c., and the greater portion of the following pages will be devoted to the functions of these various forms of cells.

So long as a cell remains in its indifferent stage it possesses the properties of ordinary protoplasm only ; but by its further development it acquires special properties not common to all protoplasm. These properties may or may not be accompanied by structural change. Thus the protoplasm of a gland-cell differs in little from that of any other cell except in the capabilities of its nutritive changes and its chemical products ; while on the other hand, those epithelial cells which form the outer layer of the skin lose their protoplasmic characters and are completely modified in structure.

TISSUE DIFFERENTIATION.

The first stage in the existence of any organism, from the simplest form of plant to man, consists of a single cell (in animals called the ovum or egg), which differs in no essential points of structure from an ordinary cell.

There is moreover a class of organisms in which the individuals never go beyond this stage, but pass their entire life-time in the state of a simple unicellular organism. The individuals composing this group (*Protista*), though insignificant in point of size, may vie with the higher plants and animals in number, species, and variety of form, so that they might well be placed in a kingdom by themselves (as has been proposed) apart from the vegetable and animal kingdoms.

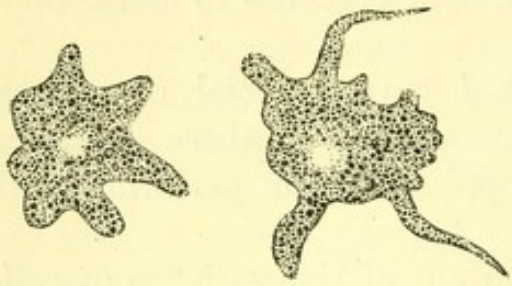


Fig. 6.—Unicellular organism. Small amœba. (Cadiat.)

The group of these organisms which most resembles animals, is called *Protozoa*, and is divided from other animal forms by the

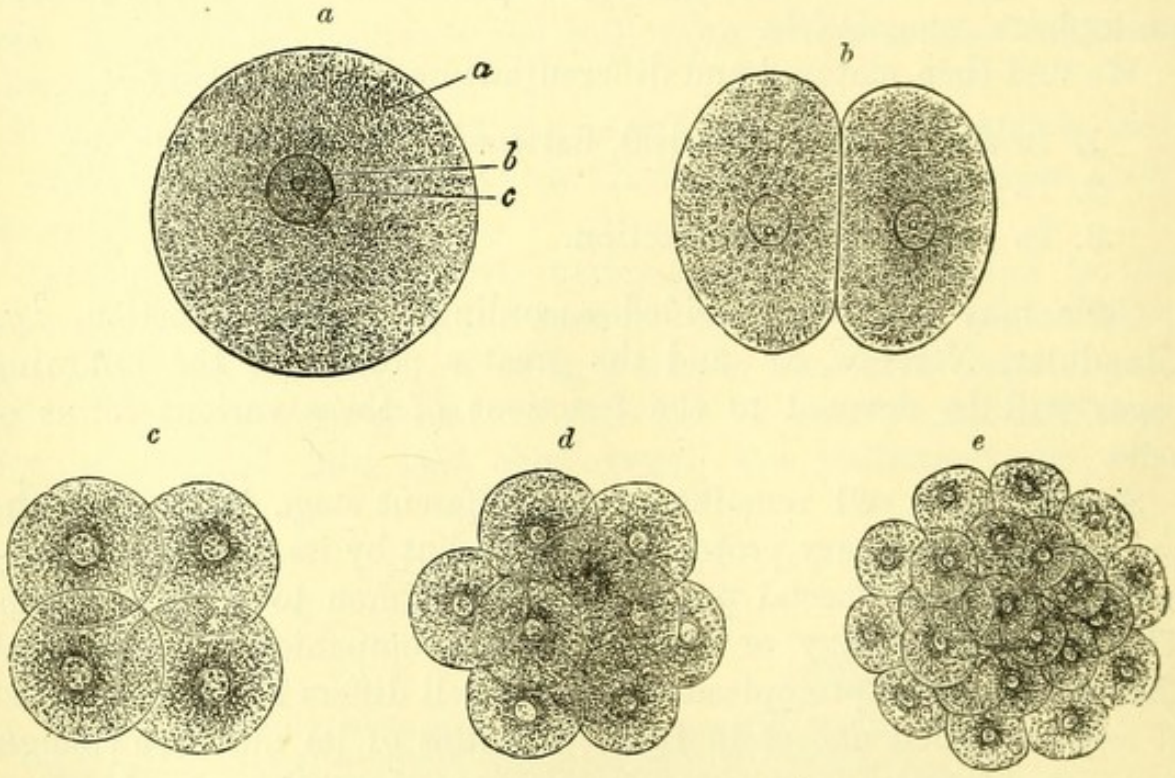


Fig. 7.—Stages in the division of the egg cell (ovum), showing the production of a multiple mass by division. (Gegenbauer.)

manner of development of the ovum of the latter, which divides into cells that subsequently become differentiated into tissues. This group is called the *Metazoa*.

In the Protozoa the ovum never divides, the animal always remaining a single cell. On the contrary, the ovum of the Metazoa changes its characters during its development. At first possessing a stage common to both divisions, viz., a single cell, it soon passes

though rapid stages of cell proliferation, and is converted into a multiple mass, the mulberry stage or *Morula*.

The cells forming this Morula stage approach the periphery of the mass, where they arrange themselves in two layers, and form a cavity in the centre. This is known as the *Gastrula* stage. Following then this cell multiplication we find a qualitative differentiation of the cells, by which certain groups of cells assume special peculiarities, fitting them for some specific duty.

Thus we arrive at the production of special textures and organs such as are met with in the higher animals, and which are necessary for the efficient discharge of the various functions carried on during their lives. The division of the original mass of indifferent cells into two layers of special cells is the first step towards tissue differentiation, and in some animals is the only one arrived at in their life history, throughout which they remain a simple sac made up of an external layer, *Ectoderm*, and an internal layer, *Endoderm*.

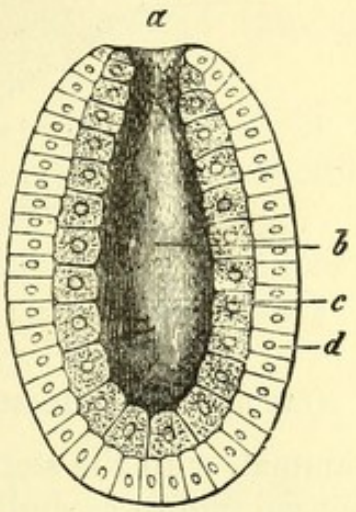


Fig. 8. — Diagram showing the first differentiation of the organism into an external and internal layer. (*a*) Mouth, (*b*) alimentary cavity, (*d*) ectoderm, (*c*) endoderm. (Gegenbauer.)

The groups of cells forming the outer and inner layers of this stage of development, not only form the primitive tissues, but also represent the first appearance of organs or parts with a specific function. The external or ectodermic layer is the supporting protecting, motor, and respiratory organ, while the inner or endodermic layer is devoted to a primitive form of digestion, preparing the food for assimilation, and generally presiding over the nutrition of the body.

Although this sac-like (Gastrula) stage is supposed to have formed a step in the life history of nearly all animals, yet it forms a less striking part in the development of the individuals as we ascend the scale, and in the higher animals no such stage has been recognised. In the Vertebrates, the germ-cells derived from the ovum are from an early period divided into three distinct layers, as those which correspond to the Ectoderm and Endoderm of the lower organisms, form between them a third layer or *Mesoblast*.

From these germinal layers all the organs and tissues of the body are subsequently evolved. In embryological language the three primitive layers are called *Epi-*, *Meso-*, and *Hypo-blast*.

Thus it can be seen that, as we can compare the primitive unicellular state of the lowest animals with the first egg-cell stage of existence of the highest animals, so we can compare all the steps of tissue and organ differentiation as we trace them in the embryo of a

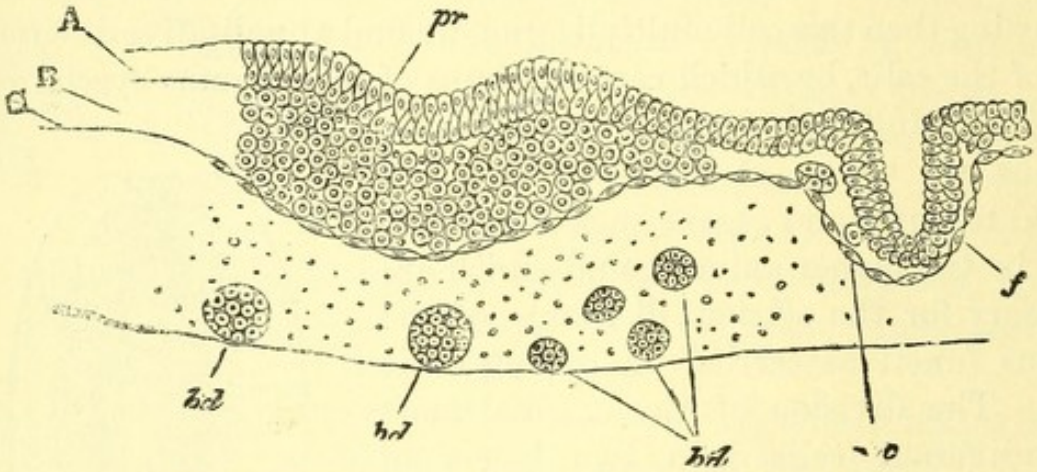


Fig. 9.—Transverse section of blastoderm of chick.
A. Epiblast. B. Mesoblast. C. Hypoblast. *pr.* Primitive groove.

mammal, with the steps of elaboration in organic and textural parts that we find in ascending the scale of animal life.

The history then of the development of any mammal from a single cell or egg to the complex adult individual, is analogous with the more protracted history of the evolution of the animal kingdom from the Protista upwards.

It is impossible to separate the differentiation of tissues and organs, or to say which is of older date in the history of animal evolution. Even in unicellular animals, where we have no trace of tissue difference (Paramæcium, Vorticella), there being only one cell, we have a distinct foreshadowing of organ and functional differentiation (vide Chapter III.). And in creatures made of many parts, the same cells have several duties to perform. But when an aggregation of specialised cell-units exists, it may be said to be a tissue. If these cells have no very special characteristic, then the tissue may be called primitive or embryonic. But, as has just been stated, the aggregation of embryonic cells—in the higher forms of life—have special characters from the very first, which mark them off from one another as destined for different functions.

The middle germ layer (mesoblast) is derived from the upper (epiblast) and lower (hypoblast), the relative amount contributed by each being doubtful. From the earliest period the middle layer has distinctive characteristics, and ultimately gives rise to a set of tissues which can always be distinguished from those which originate from the upper and lower layers.

From the inner and outer germ-layers are formed several connective tissues, which, in a more or less perfect degree, retain the activity of the original protoplasm, and hence may be called *active tissues*. From the middle germinal layer is developed a set of textures, in the majority of which the protoplasmic elements are reduced to a minimum, and are therefore grouped together as *supporting tissues*.

The tissues formed in the adult may be classified into four groups.

1. *Epithelial Tissues.* The primitive surface tissues of the epiblast and the hypoblast, which are variously modified for several distinct functions.
2. *Nerve Tissues.* Springing from the former, are modified for receiving, conducting, controlling, and distributing impressions.
3. *Muscle, or Contractile Tissues.* In close relation to both the previous and the next groups.
4. *Connective Tissues* formed only from the middle germ-layer. They are much modified in different parts, so as to give shape to the body, and to support and hold the various organs and parts firmly together. They are, in fact, the materials used in the general body architecture.

Epithelial Tissue, although the oldest kind of tissue both in the animal series and in the germinal layers, retains the embryonic character of being entirely composed of cells placed in close relationship on the internal and external surfaces of the body. The individual cells retain the embryonic character in form and function, being soft rounded masses of protoplasm, only altered in shape by the pressure of their neighbours. The cells which lie next the nutrient vessels of the mesoblast, are endowed with energetic powers of growth and reproduction. As the young cells are produced they take the place of the parent cell, whose future life-history determines the special characters of the different kinds of tissues.

Sometimes the cells are retained, as in the skin, and are arranged in several layers, one over the other. As the cells are conveyed from the deeper layer, where they take their origin, towards the surface, the efforts of the waning nutritive power of the protoplasm are devoted to the manufacture of a tough insoluble substance. The cells thus gradually lose their vital activities, and are converted into horny scales, which form the external protecting skin, and its many modi-

fications that give rise to the different dermal appendages, such as hair, feathers, &c. Instead of a horny substance, the protoplasm

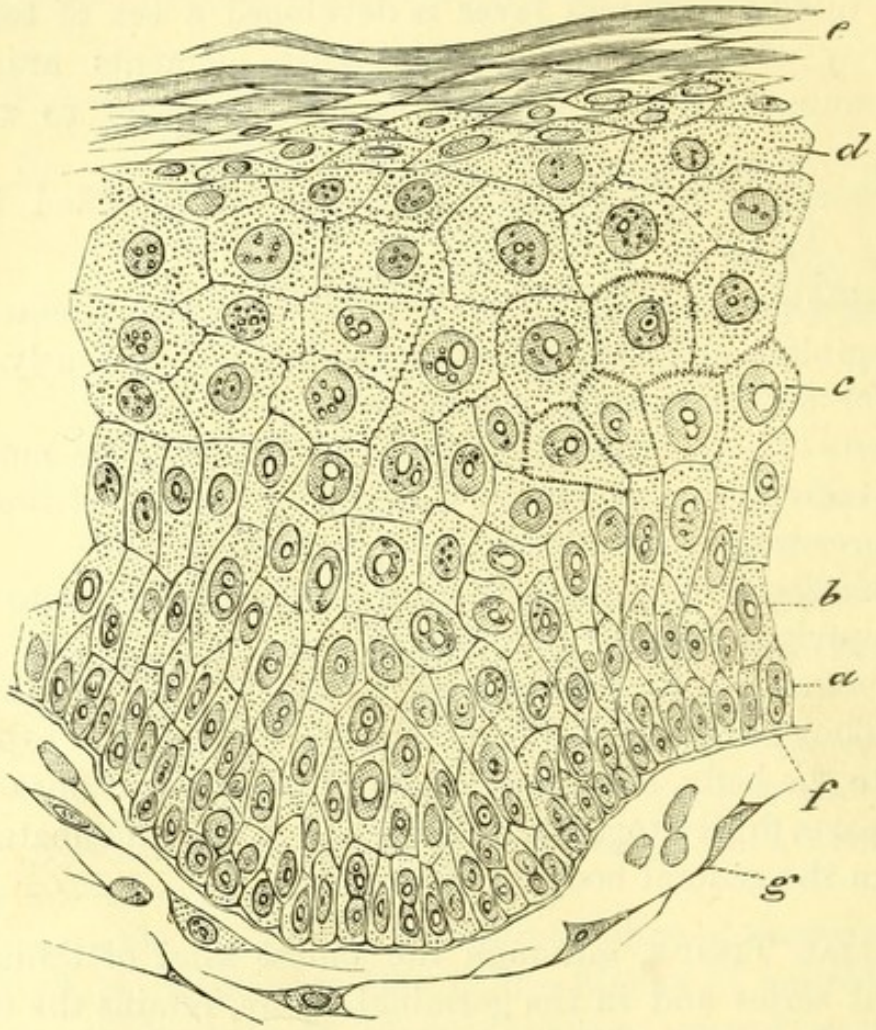


Fig. 10.—Section of the epiderm of the prepuce showing the super-imposed layers of cells of a stratified epithelium. (Cadiat.)

a. Young proliferating cells. *b*—*d*. Cells advancing towards surface. *e*. Flattened cell of horny layer. *f*. Basement membrane. *g*. Connective tissue.

may manufacture fat in the bodies of the cells, as seen in the mammary and the sebaceous glands of the skin. In other cases the reproductive activity of the cell is in abeyance, and its nutritive energy is devoted to the manufacture of a material which is poured out of the cell at certain periods. Thus we have another function performed by the epithelial tissues, namely, that of manufacturing certain materials which, being collected by suitable channels, appear as secretions.

The active elements of glandular tissue are epithelial cells whose nutrition leads to the formation of specific chemical products within their protoplasm. These products pass out commonly as fluids, and

form various substances of great importance in the economy. A gland is simply a special arrangement of epithelial cells

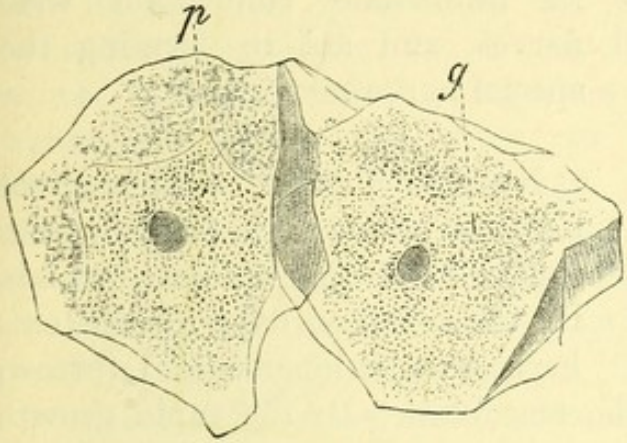


Fig. 11.—Two cells of scaly epithelium from the inside of the cheek. (Ranvier.)

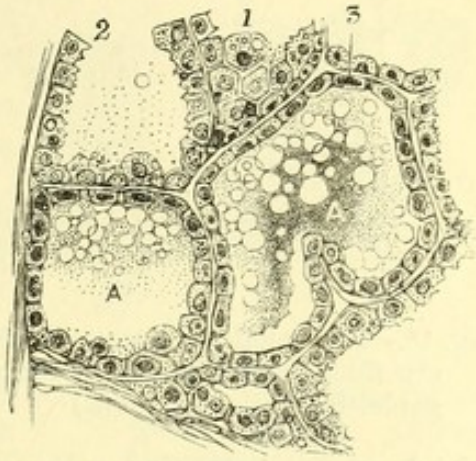


Fig. 12.— Section of milk-gland of cat, showing secreting cells containing fat globules, and some secretion in alveoli.

lining the sacs or tubes into which the secretion is poured. Some tracts are covered with fine moving hair-like processes, called cilia, which give rise to a slight motion of the fluids in contact with them.

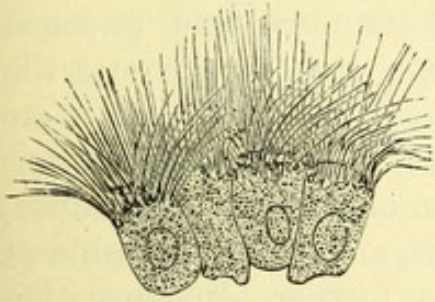


Fig. 13.—Ciliated epithelial cells from the gills of mussel. (Cadiat.)

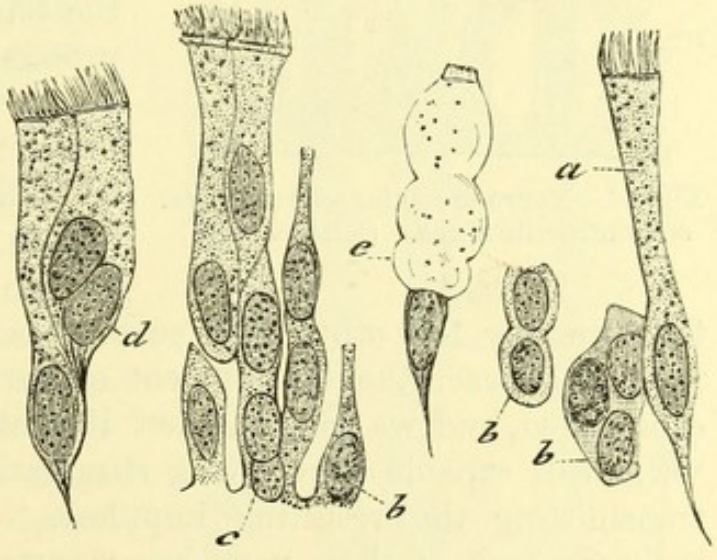


Fig. 14.—Stratified ciliated epithelial cells from the trachea of man. (Cadiat.)

a. Large surface cells, with cilia on surface.
b. Lower cells in earlier stage of development.
e. Cell charged with mucus.

The epithelium in various places is thus seen to be modified in different ways, so as to make it suitable for the special function of the part in which it is placed.

Other differences will be given in detail with the description of the uses of the many mucous surfaces. The most interesting modifications are those in the special sense organs, where the cells are in immediate connection with nerves, and aid in forming the special nerve terminals.*

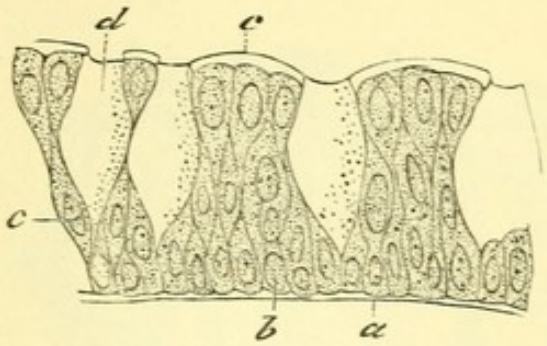


Fig. 15.—Epithelial cells, some of which are filled with mucus (*d*), forming goblet-like cells. (Cadiat.)

Nerve Tissue. — The great nervous centres are formed from the cells of the epiblast, which, in the earliest days of the embryo, form a longitudinal furrow, which sinks into the cells of the mesoblast. By the rapid growth of the latter the depressed part is cut off from the rest of the epiblast, and forms the rudiment of the spinal cord and brain. In looking for special conducting tissue in animals possessing the most simple structure, we find cells which would seem to possess certainly a two-fold, and possibly a three-fold function,—one of which is conduction. In the so-called "neuro-muscular" cells of the hydra, processes are described as passing off from them, and uniting beneath the ectoderm with other fibre-like processes, which are evidently contractile. Here we find for the first time a portion of protoplasm specially devoted to acting as a conductor of impulses, and attached by the one end to a contractile fibre, and by the other to a surface (sensory) cell. The intimate relation between the development of nerve and muscle fibres is thus established, and we have the first indication of a nerve mechanism, viz., a cell capable of receiving stimulations, and a fibre capable of transmitting the resulting impulses. As further differentiation proceeds, each of these parts becomes more distinct from the other, and ultimately the adult nerve tissue is found to be made up of nerve fibres, and special cells, forming nerve endings.

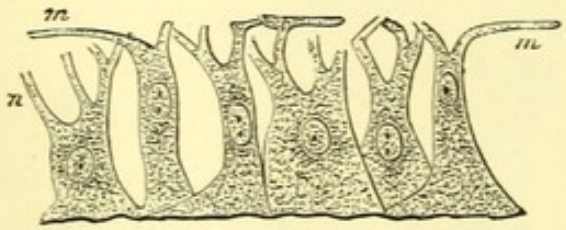


Fig. 16.—Neuro-muscular cells of hydra. *m*. Contractile fibres. (Kleinenberg.)

The fibres act as lines of communication between ganglion-cells: they connect together the numerous cells in the various parts of the brain and spinal cord, or pass between those of

* A further account of the Histology of these tissues will be found in the chapters specially devoted to these subjects.

the central nervous organs and ganglia distributed throughout the body, which might be called the peripheral nerve-organs.

The simplest idea then of a special nerve apparatus is a fibre connecting two cells. The peripheral cell may be a receiving organ (fig. 17, s), from which, when stimulated, impulses are transmitted along the fibre to the central nerve cell, where they give rise to certain impressions, and so we have a sensory nerve apparatus. Or the central nerve cell may be the receiving agent, getting stimuli from its central neighbours, and transmitting impulses to a peripheral nerve terminal, by which they are handed over to a muscle (M) or gland, and thus we have a simple motor or secretory apparatus.

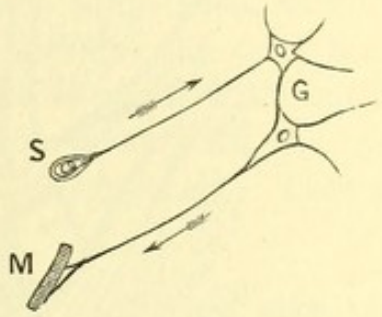


Fig. 17.

S. Sensory receiving organ with attached afferent nerve-fibre.
G. Central organs — ganglion cells.
M. Peripheral organ and efferent nerve.

Where the effect of a stimulus can be definitely traced from one nerve cell to another, and from thence by a second fibre to a third cell, the impulse is said to be reflected by the second cell to the third. And there we have what is called a *reflex act*.

The essential part of a nerve fibre is a kind of protoplasmic band, in which the finest fibrilla or thread-like marking can be made out with the aid of reagents and a powerful microscope. This is called the *axis-cylinder*. In some nerve fibres (mostly in the brain and spinal cord) the axis-cylinder is naked, and even a single fibril may so pass from one cell to another in the brain matter. In other parts the axis cylinder is generally covered by a thin membrane, called the *primitive sheath*, or with a soft oil-like substance, called the *medullary sheath*, or, as is commonly the case in most peripheral nerves, by

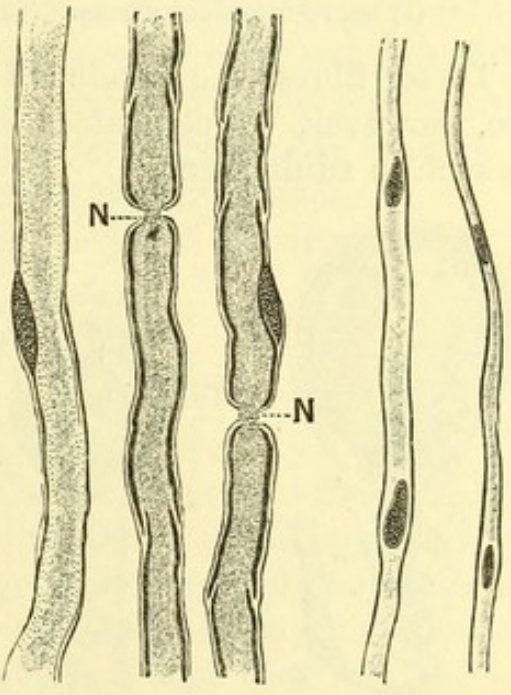


Fig. 18.—Three medullated nerve-fibres, the medullary sheath of which is stained dark with osmic acid. N, Nodes of Ranvier.
Two non-medullated nerve-fibres, with nuclei in the primitive sheath.

both. The primitive sheath encloses the medullary sheath, which surrounds the axis-cylinder.

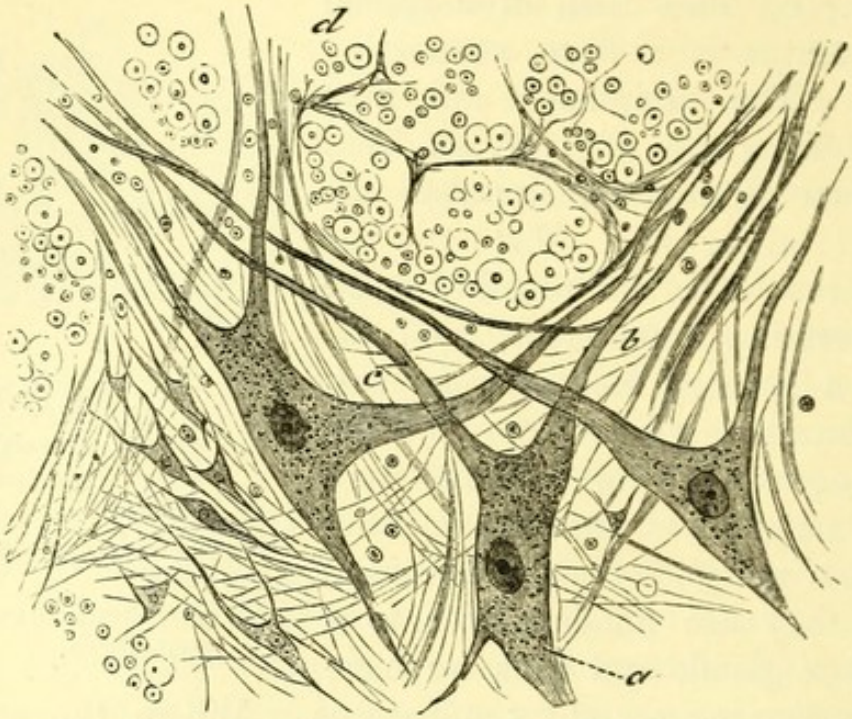


Fig. 19.—Multipolar cells from the anterior grey column of the spinal cord of the dog-fish (*a*) lying in a texture of fibrils; (*b*) prolongation from cells; (*c*) nerve-fibres cut across. (Cadiat.)

These fibres are made of peculiarly modified cells, which are, however, so elongated as not to be very easily recognised as such in adult tissue.

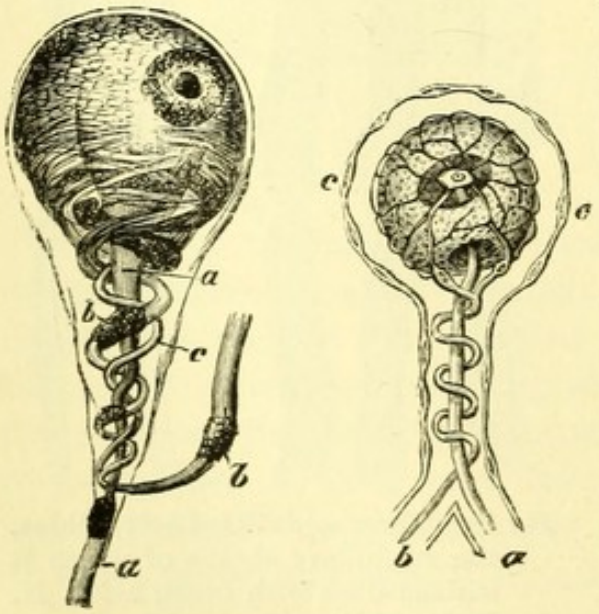


Fig. 20.—Ganglion cells of frog, showing straight and spiral fibres. (After Beale and Arnold.)

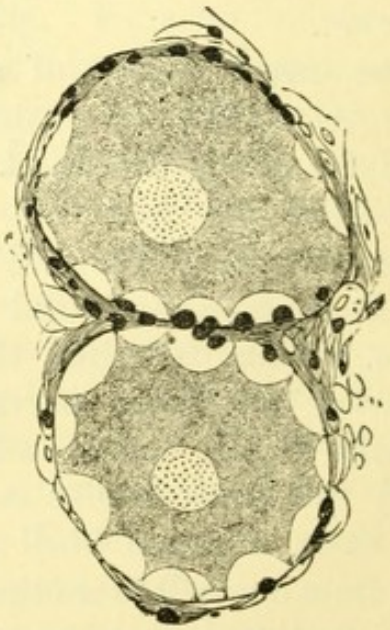


Fig. 21.—Cells from the sympathetic ganglion of a cat. The protoplasm is retracted here and there from the cell-wall.

The nerve or ganglion cells vary extremely in general form and size. The commonest in the nerve centres are large bodies with a

clear, well-defined, vesicular, single nucleus, and distinct nucleolus; they have two or more processes, which are connected by nerve fibres to other cells, and to the axis-cylinder of nerves.

The peripheral nerve cells are generally much modified, and often small compared with those in the centres. Besides the cells in the sporadic ganglia, which are large rounded corpuscles with but few processes—there are many other bodies connected with the peripheral nerves which cannot be called ganglion corpuscles. They are nevertheless nerve cells.

Muscles or Contractile Tissues.—When changes take place in protoplasm adapting it specially for contraction, it is termed muscle tissue. The large masses of this tissue attached to the skeleton so as to move its various parts, form the flesh of the higher animals. Muscle tissue is, almost invariably, connected with nerve tissue, and acts in response to stimuli communicated from the nerves. In some of the lower animals the two tissues are so intimately related that it is not easy to distinguish them, and the development of both progresses equally as we ascend the scale of animal life. They are nearly related in their origin, or even spring from the same primitive tissue. In fact, as has already been mentioned (*vide* p. 20), they form but one structure in some of the more simple and less differentiated animals. The neuro-muscular tissue, which is formed from the outer layer of the embryo, is the forerunner of the muscles as well as of the nerves of the embryo of the higher animals.

In the higher animals and man muscle tissue consists of two distinct kinds of textures, known as—

a. Smooth, or non-striated muscle.
b. Striated muscle.

In the smooth muscle the individual elements present the characters of an elongated and flattened cell, and contain a single long nucleus. They contract very slowly, and require a comparatively long time for the nerve influence to affect them, so that an obvious interval exists between the moment of their stimulation and their contraction. They are found in the internal organs and in situations where gradual and lasting contractions are required. They receive their nervous supply generally from the sympathetic system, and perform their duty without our being conscious of their activity or being able to control it by our will.

Striated muscle tissue is made up of cylindrical fibres of such length that both extremities cannot be brought into the field of the

microscope at the same time. Their exact relation to cells is not so easily made out as in smooth muscle, and doubtless varies in different

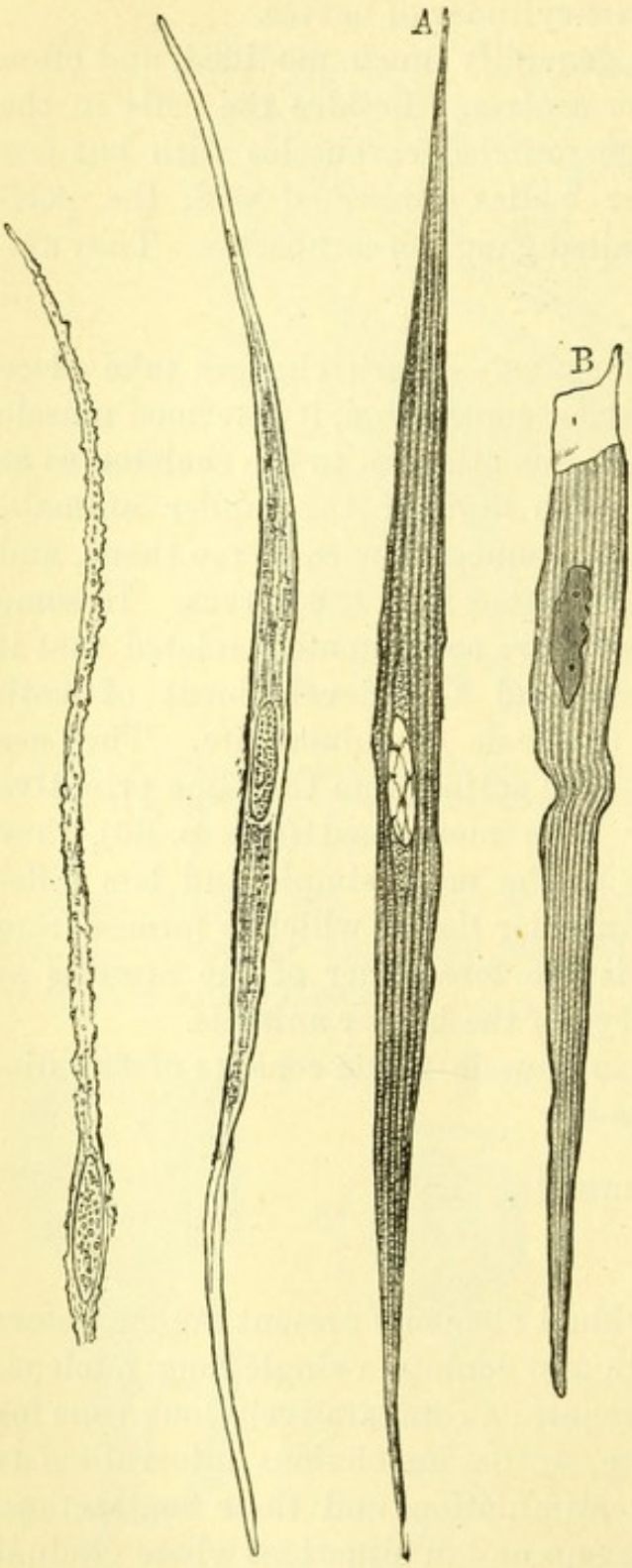


Fig. 22.—Cells of smooth muscle-tissue from the intestinal tract of rabbit. (Ranvier.)

A. and B.—Muscle-cells in which differentiation of the protoplasm can be well seen. (Schäfer.)

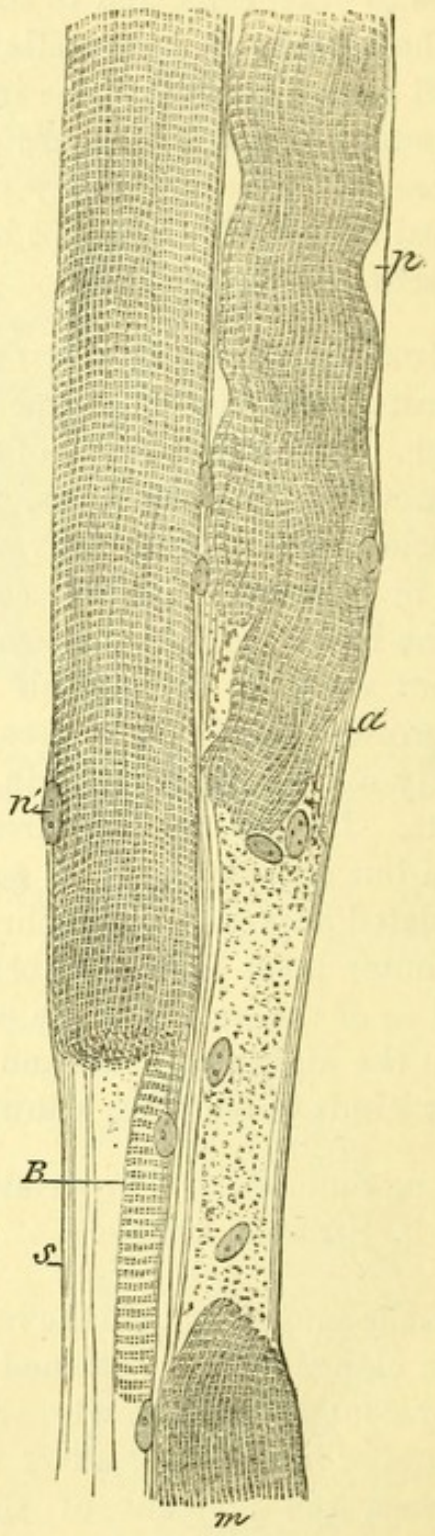


Fig. 23.—Two fibres of striated muscle, in which the contractile substance (*m*) has been ruptured and separated from the sarcolemma (*a*) and (*s*); (*p*) space under sarcolemma. (Ranvier.)

muscles. Sometimes the fibres are made up of single cells, and in other cases they are formed by the permanent fusion of several cell-

elements which never differentiate into separate elements, owing to the imperfect division of the cells, but make up one mass, the multiple nuclei of which alone make its mode of origin apparent. The contractile substance is made up of two kinds of material, one of which refracts light singly, while the other is doubly refracting. These are ranged alternately across the fibre, making the transverse markings or striæ from which it gets its name. This striated material is quite soft and is encased in a thin homogeneous elastic sheath called *sarcolemma*, which fits closely around the soft contractile substance.

This form of muscle is the widest departure from the primitive protoplasmic type, being specially modified so as to perform strong and quick contractions. It moves with wonderful rapidity, contracting almost the instant its nerve is stimulated. It forms the great mass of the quick-acting skeletal muscles, being attached to the bones by bands composed of a form of fibrous tissue, which form the tendons and fasciæ. Muscles made of striated tissue are commonly under the control of the will, and hence are frequently spoken of as voluntary muscles, but this term is misleading, for many striated muscles are not governed by voluntary control.

The Connective Tissue group, coming exclusively from the mesoblast, exhibits very great varieties of form. Its cells differ much from the epithelial cells both in their character and their relations, and particularly in the adult tissues.

Under the heading Connective Tissues are generally classed all those which support the frame and hold together the various other tissues and organs. They are—

1. Mucous and retiform connective tissues.
2. White and yellow fibrous tissue.
3. Cartilage.
4. Bone.
5. Endothelium.

The cells of all these tissues have the property of manufacturing some material which does not generally enclose them as a cell-wall, but remains between the cells and forms the intercellular substance. The younger the tissue the greater is the proportion of its cellular constituents, and the older the tissue the greater will be found the preponderance of the intercellular substance.

Mucous Tissue.—In certain parts of the embryo and in some of the lower animals a kind of connective tissue is found in which there

is but little intercellular substance, the mass of the tissue being thus made up of cells. The cellular connective tissue never forms an important texture in the adult, but is interesting as the probable tissue from which the connective tissues are formed in the embryo, and as occurring in abnormal growths or tumours.

The first step in its differentiation is the secretion of a large quantity of soft homogeneous, semi-gelatinous or fluid material like the mucus secreted by epithelium. In this the cells lie, either free

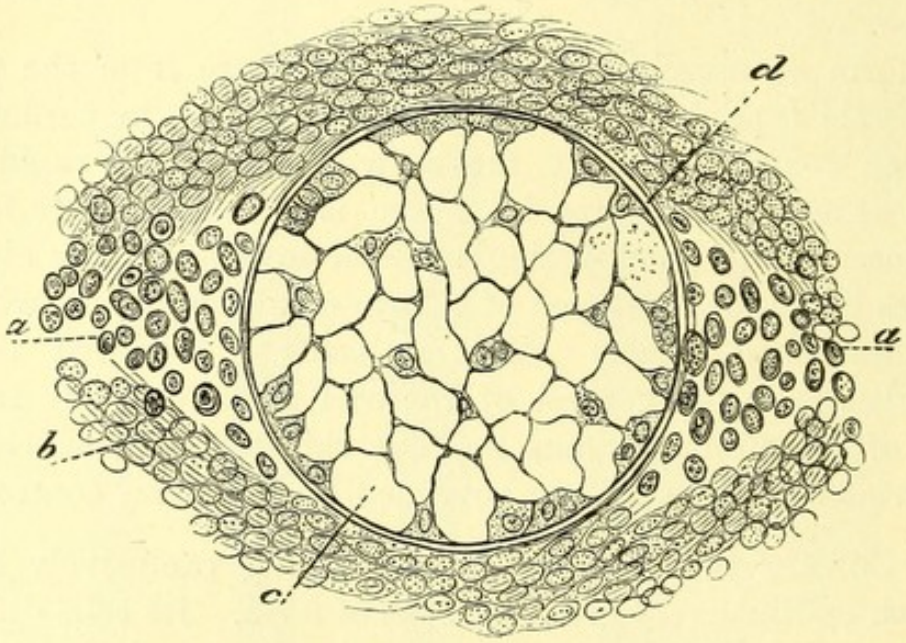


Fig. 24.—Transverse section of the chorda dorsalis and neighbouring substance. *a*, cartilage cells; *b*, cell of the middle layer of embryo; *c*, mucous tissue; *d*, boundary of chorda. (Cadiat.)

or united by long protoplasmic processes. The processes uniting the cells may not be present, and the cells may be reduced to a minimum, as occurs in the vitreous humour of the eye. But more commonly the soft gelatinous substance is reduced in amount, and the processes connecting the cells are converted into a dense network of delicate threads to form the retiform tissue of lymphoid structures.

White Fibrous Tissue.—The cells of the last described variety may become differentiated by a process of fibrillation. The growth of the cells leads to the formation of a fibrillated substance which ultimately forms the great bulk of the tissue, while the cells become gradually and proportionately fewer in number. In this case only sufficient of the mucous substance generally remains to cement the fibrils together into bundles. A few of the cells, however, remain between the bundles of fibrils to preside over the nutrition of the tissue. Thus is formed the non-elastic or white fibrous tissue of tendon.

These fibrils of white fibrous tissue are easily affected by chemical re-agents. Weak acids cause them to swell up and become indistinct. Baryta water affects the cement and renders them easily

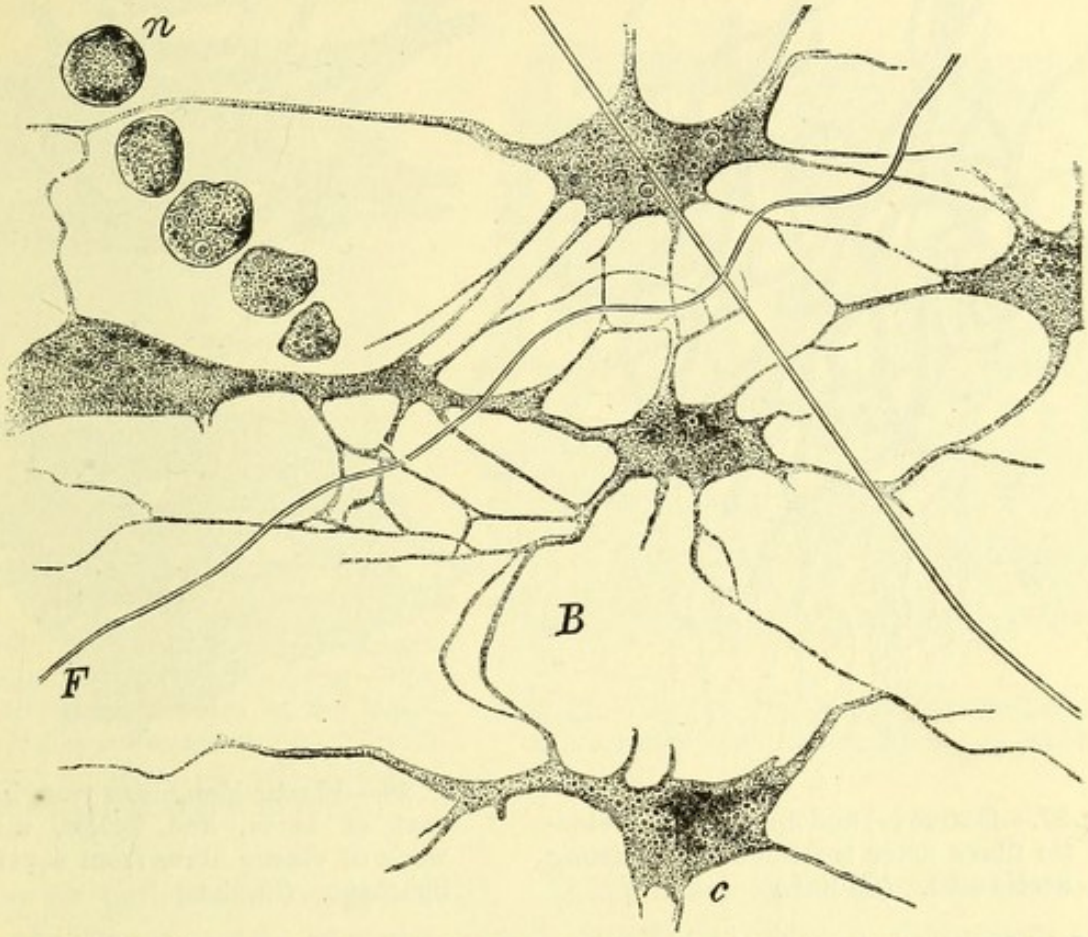


Fig. 25.—Cells of mucous tissue with branching processes (B) and a couple of elastic fibres (F). (Ranvier.)

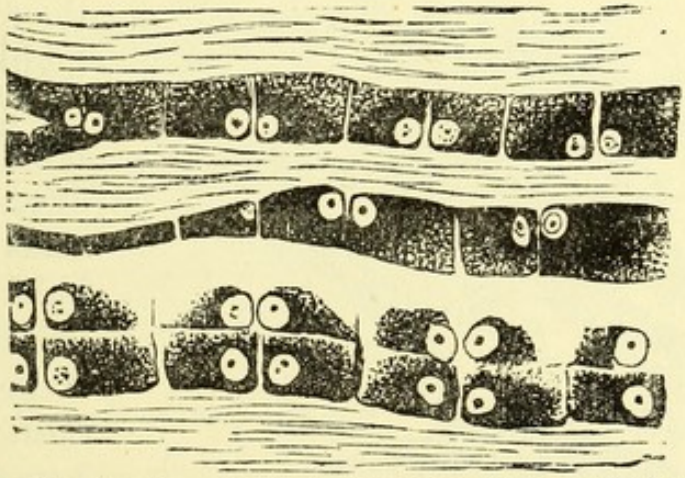


Fig. 26.—Portion of tendon from the tail of a young rat, stained with gold chloride, showing arrangement of flattened cells on bundles of fibrils. (After Klein.)

separable. They swell and dissolve in boiling water, yielding gelatine, which forms a jelly on cooling.

YELLOW ELASTIC TISSUE. — In some parts of the body

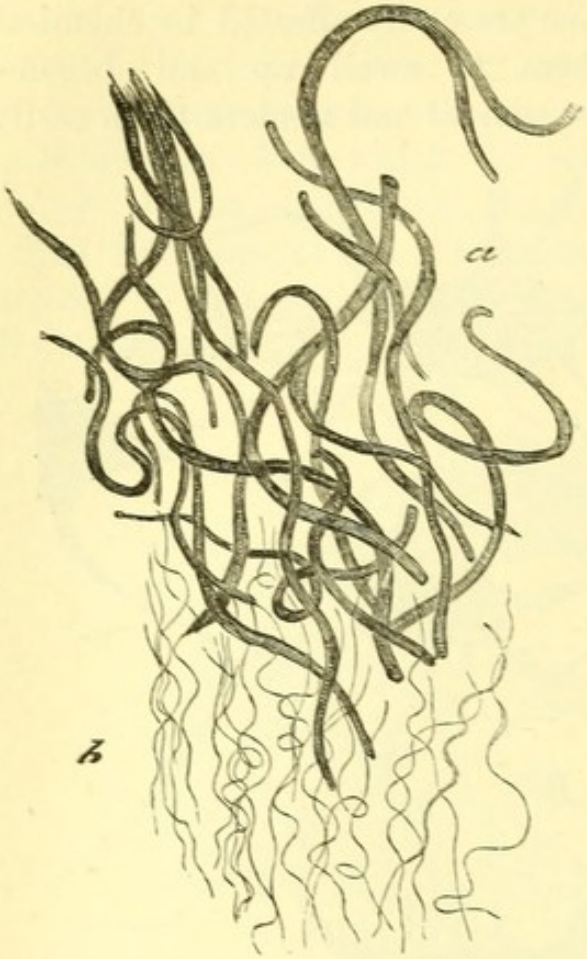


Fig. 27.—Coarse (*a*) and fine (*b*) yellow elastic fibres after treatment with strong acetic acid. (Cadiat.)

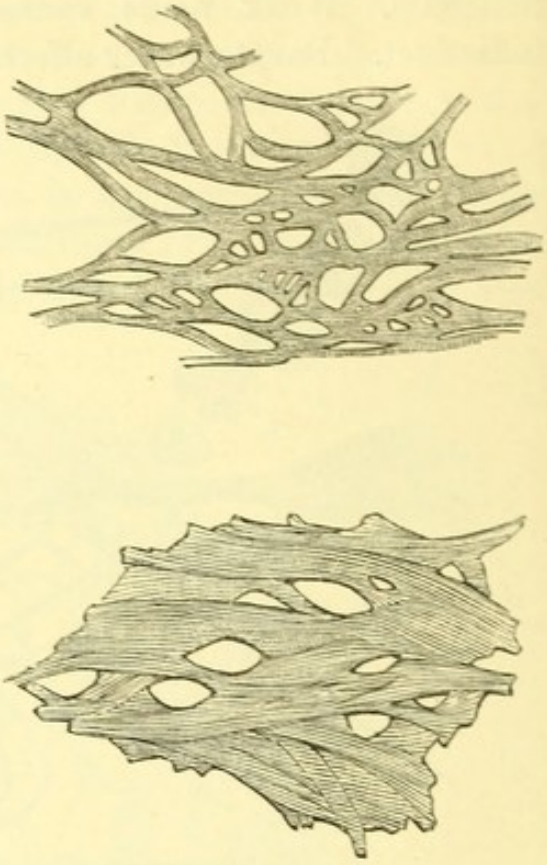


Fig. 28.—Elastic membrane from inner coat of aorta, and, below, meshwork of elastic fibres from a yellow ligament. (Cadiat.)

a kind of intercellular substance is formed, which differs in many respects from the foregoing. It is highly elastic, does not give gelatine on boiling, and is not affected by weak acids or alkalis. In bulk it has a pale yellow colour, and is spoken of as *yellow elastic tissue*. It is sometimes found alone forming an elastic band or ligament, but more commonly mingled with fibrillar tissue to form the connecting medium which lies under the skin and between the various other textures.

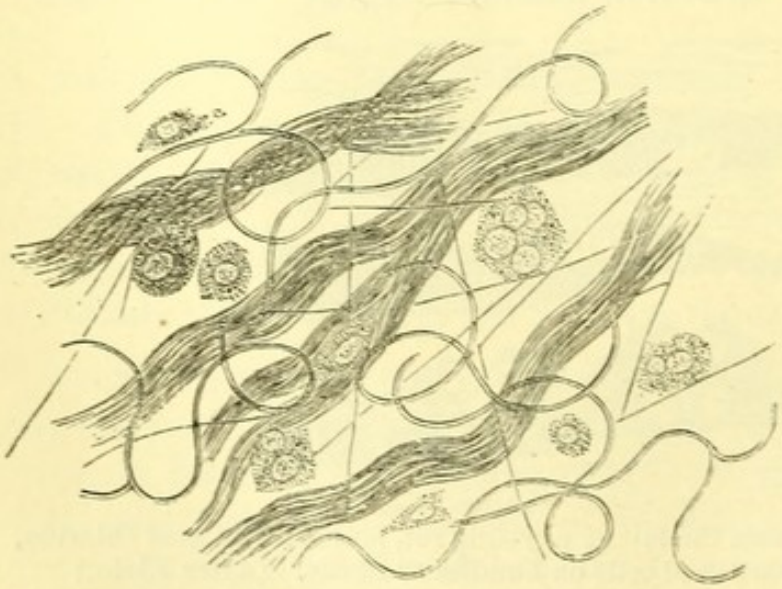


Fig. 29.—A teazed preparation of connective tissue showing fine and coarse elastic fibres mingled with bundles of fibrillar tissue and connective tissue corpuscles.

CARTILAGE.—In this tissue the intercellular substance secreted by the cells is hard, and forms in the earlier stages of its development

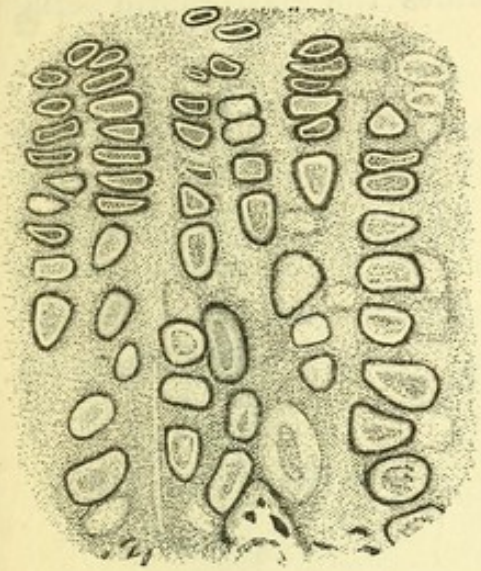


Fig. 30. Section of hyaline cartilage from the end of a growing bone, showing a decrease in the intercellular substance compared with the number of cell-elements, which are arranged in rows.

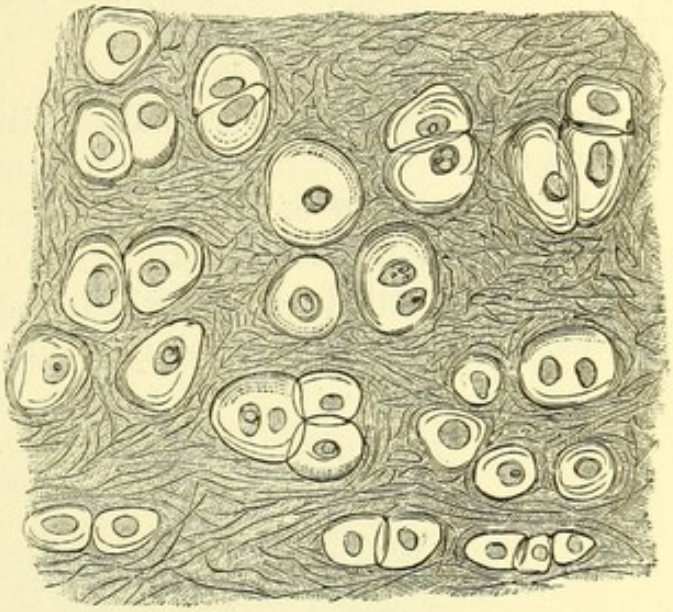


Fig. 31.—Elastic fibro-cartilage, showing cells in capsules and elastic fibres in matrix. (Cadiat.)

cases or cell-walls for the cells. These cases subsequently increase in thickness, and become fused together into a homogeneous

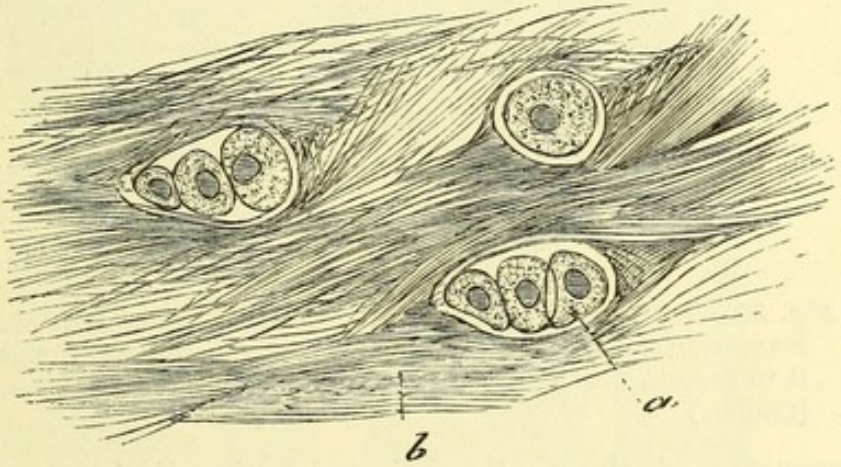


Fig. 32.—White fibro-cartilage, showing cells (*a*) in capsules and fibrillar matrix (*b*). (Cadiat.)

intercellular substance, where ultimately the areas belonging to the different cells can no longer be distinguished from one another, so that in the adult tissue there is a tough matrix of intercellular substance, in which the cells are scattered, apparently occupying small

cavities. These cells preside over the nutrition of the tissue. The intercellular substance, which is quite homogeneous in common hyaline cartilage, is sometimes modified so as to resemble fibrous tissue, sometimes the fibrillar, and sometimes the elastic form being produced. (Figs. 31 & 32.)

Bone.—This is the most marked differentiation of the connective tissue group. The intercellular substance is characterised by containing a great quantity of earthy or inorganic matter (65 %), which gives the bone its enormous strength. The cells of the tissue are enclosed in little cavities called *lacunæ*, which are related by minute canaliculi to each other. The intercellular substance is everywhere traversed

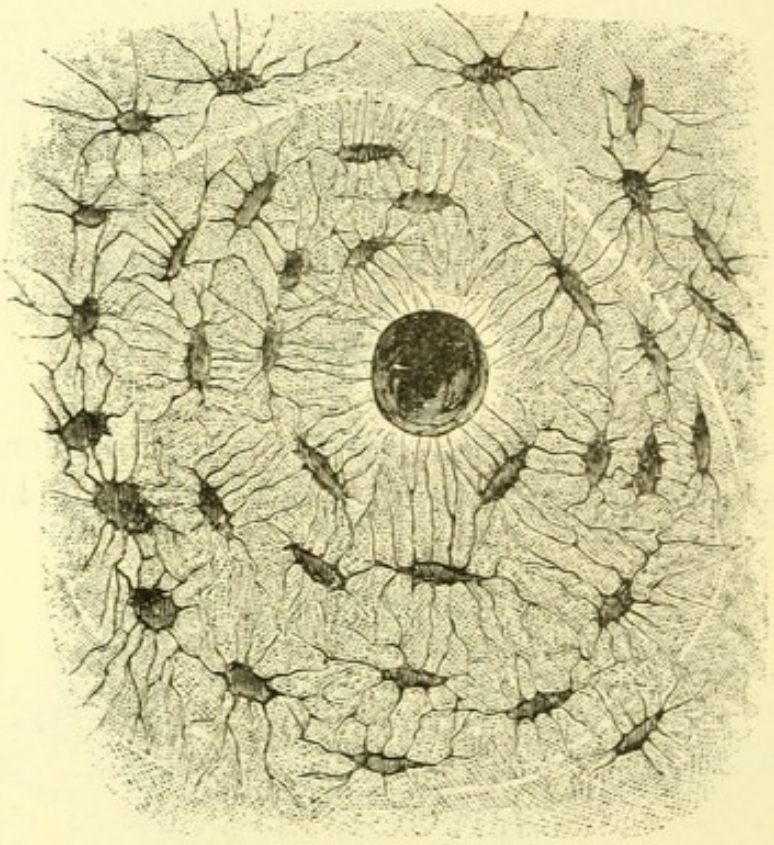


Fig. 33.—Transverse section of a system of Havers, showing Haversian canal in centre, with bone-cells arranged around it in *lacunæ*, which are connected by the delicate *canaliculi*. (Cadiat.)

by the processes of the cells lying in the little canals which connect the lacunæ, and thus the adequate nutrition of the tissue is secured. Chemically, bone tissue consists of about :—

Calcium phosphate	53
Calcium carbonate	11
Magnesium phosphate, calcium fluoride and soda salts	1
Gelatine yielding animal matter	33

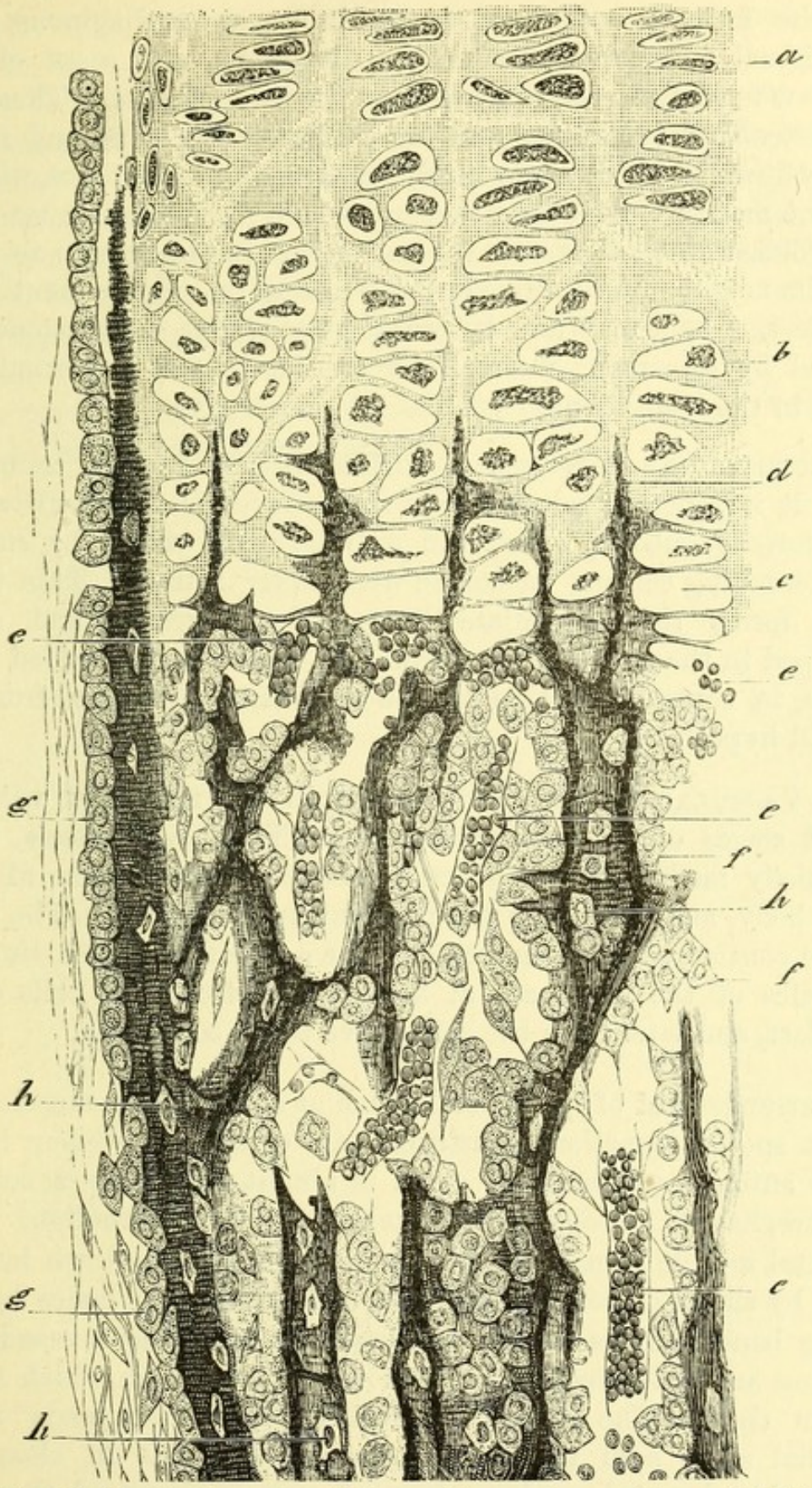


Fig. 34.—Section through ossifying cartilage and young bone. (Cadiat.)

a. Cartilage cells.
b. Degenerating cartilage cells.
c. Cell space, empty.
d. Spiculæ of calcareous deposit.
e. Blood corpuscles.
f. Osteoblasts.
g. Ditto of periosteum.
h. Bone-cells.

In the formation of bone from fibrous or cartilaginous tissue the original intercellular substance disappears, and a set of cells with new formative powers come upon the field (Fig. 34.) These new cells (osteoblasts) cover the growing surface of the bone and secrete and lay down in layers a new kind of intercellular substance, which is the bone matrix. Here and there, at wonderfully regular intervals, an osteoblast ceases to secrete the calcareous intercellular substance, while its neighbours continue formative activity. Consequently, this osteoblast, or as it may now be called young bone cell, becomes surrounded by calcareous intercellular substance, and is permanently lodged in the bone tissue.

Endothelium.—Wherever a surface occurs in the connective tissues it is generally covered by a single layer of thin cells with a characteristic outline, which can only be made visible by staining the intervening cement substance with silver nitrate. This tissue, which forms the immediate lining of all vessels and spaces developed in the tissues arising from the mesoblast, is called *endothelium*, in contradistinction to the *epithelium* developed from the epi- and hypo-blast.

The Vascular System is developed in the mesoblast with the earliest stages of the connective tissue. The blood vessels, which are chiefly made up of connective tissues, soon traverse all parts of the body, and distribute the nutrient fluid or blood. The blood may be considered as an outcome of the connective tissues, since the corpuscles of the blood are at first formed from the cells of the mesoblast, and later from the connective tissue corpuscles.

An arrangement of special cells, such as epithelial or muscle cells, with a special function, constitutes an organ. However, in the higher animals and man an organ is almost invariably a complex structure, having various tissues entering into its construction. Thus a skeletal muscle is made up of a quantity of muscle fibres held together by sheets of connective tissue, and attached to bones by connecting bands. It is further traversed by many blood vessels, and the fibres are in immediate relation to certain nerves which terminate in them. The various secreting organs are made up of epithelial cells, held together by connective tissue in close relation to blood vessels and nerves, and are so arranged that they pour their secretion into a duct. The bones, which are the organs which give the body support, contain in addition to the bone tissue of which they are composed, a great quantity of indifferent

cells, fat cells, nerves and blood vessels. They are covered on the outside with a tough vascular coat, which gives them strength, assists their nutritive repair and reproduction, and acts as a point of attachment for the muscles and ligaments. Where the bones are in contact at the joints, they are tipped with hyaline cartilage.

If, then, we analyse anatomically the architecture of the human body, we find that it is made up of a number of complex parts, each adapted to some special function, and composed of an association of simple tissues such as the requirements of the special part demand.

The general arrangements of these organs and their modes of action will be discussed in future chapters.

CHAPTER III.

CHEMICAL BASIS OF THE BODY.

It seems natural to commence the description of the molecular changes that take place in the various tissues and organs of the body, with a brief account of the chemical composition of the most characteristic substances found in animal textures, because none of the processes of cell life, or tissue activity, can be satisfactorily studied without familiarity with the more common terms occurring in physiological chemistry.

The chapter on this subject here introduced, is intended rather to give the medical student a general view of the chemical composition and characters of the substances most frequently met with in the chemical changes specially connected with animal life, than to supply a complete or systematic account of the relationships of the chemical bases of the body, for which reference must be made to more advanced text-books, or treatises on the special subject of physiological chemistry. This review must, for the sake of brevity, be inadequate in the case of many substances, but these will be again referred to when speaking of the function with which they are associated.

It has already been stated that of the seventy elements known to chemists, a comparatively small number form the great bulk of the animal body, although traces of many are constantly present. Thus, we shall see that four elements, namely, (1) oxygen, (2) carbon, (3) hydrogen, (4) nitrogen, are present in large proportions in every tissue, and together make up about 97 per cent. of the body; and sulphur, phosphorus, chlorine, fluorine, silicon, potassium, sodium, magnesium, calcium, iron, and in certain animals copper, are indispensable to the economy, and are widely distributed, but are found in comparatively minute quantities. Occasionally traces of zinc, lead, lithium, and other minerals may be detected, but these must be regarded rather as accidental than indispensable ingredients.

The attempt to investigate the composition of a living tissue by chemical analysis, must cause its death, and thus alter the arrange-

ments of its constituents, so that its true molecular constitution during life cannot be determined.

We know that the composition of all living textures is extremely complicated, having a great number of components, most of which contain many chemical elements associated together in very complex proportions.

But as has already been pointed out, the complexity of their chemical constitution is not so wonderful as the fact, which indeed sounds paradoxical, that in order to preserve their elaborate composition, they must constantly undergo a change or renewal, which is necessary for, and forms the one essential characteristic of, their life. In fact, their complexity and instability is such, that they require constant reconstruction to make up for the changes inseparable from their functional activity.

Their chemical constituents are easily permanently dissociated, and the various components are themselves readily decomposed, generally uniting with oxygen to form more stable compounds.

The investigation of the chemical changes, known as assimilation, forms a great part of physiological study, and therefore will occupy many chapters of this book. Here we can only call attention to the chief characteristic substances to be found in the animal body, as the result of the primary dissociation or death of the textures, and briefly enumerate the products of their further decomposition as obtained by the analysis of the different substances.

The tissues of the higher animals present a great variety of substances, materially differing in chemical composition; they have all been made from protoplasm, and contain a proportion of some substance forming a leading chemical constituent of protoplasm. Every living tissue contains either protoplasm or a derivative of it, and the special characters of each tissue depend upon the greater development of some one of these substances.

It is of little use to classify the numerous chemical constituents found in the animal body in such a systematic manner as to satisfy the rules of modern chemistry, because their classification, from a strictly chemical point of view, does not set forth their physiological importance or express adequately the relation they bear to the vita phenomena of organisms.

The following enumeration of the chief chemical ingredients found in the tissues has regard to their physiological dignity as well as to their chemical construction, and will thus, it is hoped, assist the student to distinguish the different groups, and give him a better idea of their vital relationships, than a more strictly systematic classification.

A. NITROGENOUS.

I. Complex bodies forming the active portion of many tissues—Plasmata. *E.g.*, protoplasm, blood-plasma.
II. Bodies entering into the formation of and easily obtained by analysis from Group I., Albumins. *E.g.*, serum-albumin.
III. Bodies the outcome of differentiation, manufactured in the tissues by Group I., Albuminoids. *E.g.*, gelatin, &c.
IV. Bodies containing nitrogen, being intermediate, bye, or effete products of tissue manufacture. *E.g.*, lecithin, urea, &c.

B. NON-NITROGENOUS.

V. Carbohydrates in which the hydrogen and oxygen exist in the proportion found in water. *E.g.*, starch and sugar.
VI. Substances containing oxygen in less proportions than the above. *E.g.*, fats.
VII. Salts.
VIII. Water.

Class **A.** NITROGENOUS.

Group I. Plasmata.

Under this group may be placed a variety of substances which must be acknowledged to exist in the living tissues as complex chemical compounds, of whose constitution we are ignorant, since it is altered by the death of the tissue.

There are some exceedingly unstable associations of albuminous bodies with other substances, and they at once break up into their more stable constituents, albumins, fats, salts, &c., when they ar deprived of the opportunities of chemical interchange and assimilation which are necessary for their life.

Although we can only theorise as to the real chemical constitution of such substances, we must believe that they really exist in the living tissues as chemical compounds, and as chemical compounds endowed with special properties which impart the specific activity of their textures, whose molecular motions in fact are the essence of the life of the tissues.

Protoplasm: By far the most widely spread and important of these is the soft jelly-like substance, Protoplasm. This is the really active part of growing textures of all organisms, whether animal or vegetable, and forms the entire mass of those intermediate forms of life,

the protista, now generally regarded as the original fountain-head of life on the globe.

This material commonly exists in small independent masses (cells), in which we can watch all the manifestations of life, assimilation, growth, motion, &c., taking place. We must assume that this substance is a definite chemical compound ; and, further, since the living phenomena are exhibited only so long as it preserves its chemical integrity, we may conclude that its manifestations of life depend upon the sustentation of a special chemical equilibrium. Not only is this equilibrium destroyed by any attempt to ascertain the chemical composition of protoplasm by analysis, but even for its preservation the protoplasm must be surrounded by those circumstances which are known to be necessary for life, viz., moisture, warmth, and suitable nutritive material, or its destruction must be warded off by a degree of cold that checks its chemical activity.

If the chemical integrity of protoplasm be destroyed and its death produced, many new substances appear, amongst which are representatives of each of the great chemical groups found in the animal tissues. Thus, besides water and inorganic salts, we find in protoplasm carbohydrates represented by glycogen, lecithin and other fats, and several albuminous bodies, which will be described in the groups to which they belong. In addition to these, protoplasm often contains some foreign bodies which have come from without, and special ingredients of its own manufacture, such as oil, pigment, starch, and chlorophyll.

Blood-plasma : There is in living blood also a body which must be included in this group, as it undoubtedly has a much more complex constitution than any of the individual albuminous bodies, presently to be described, which can be obtained from it. This is proved by the following facts : first, its death is accompanied by a series of chemical changes, viz., disappearance of free oxygen, diminution of alkalinity, and a rise in temperature, and secondly, certain albuminous bodies appear which were not present in the living plasma.

The spontaneous decomposition of separated blood-plasma may be delayed by cold ; at freezing point the chemical processes are held in check. During life the exalted constitution of the plasma is sustained by certain chemical interchanges which go on between it and its surroundings. This question will be more fully discussed when the coagulation of the blood is described.

Muscle-plasma: Likewise, as will be found in the chapter on Muscles, there exists in the soft, contractile part of striated muscle a plasmas which at its death spontaneously breaks up into other distinct

albuminous bodies and forms a coagulum. These changes are accompanied by acidity of reaction, the disappearance of oxygen and an elevation of temperature, showing that distinct chemical change is taking place.

Oxy-hæmoglobin, the colouring matter of the blood, should be included here amongst the important chemical bodies more complex than the albumins. This singular body can be broken up into a globulin and a colouring matter *hæmatin* containing iron. It differs from all other bodies of a similarly complex nature from the fact that it readily crystallizes, and also in the very remarkable manner in which it combines with oxygen, and again yields it up.

Group II. Albuminous Bodies.

It is difficult to say how far these bodies exist as such in the living organism, but they can be obtained from nearly all parts, particularly those which contain active protoplasm, and after its death they can be detected in abundance. As may be seen, by testing for their presence in living protoplasm, the addition of any chemical re-agent or treatment causes its death, so that although albumins appear in the test-tube, this cannot be accepted as proof that they would have answered to the tests before the protoplasm was changed by its death.

They do not occur normally in any secretion except those substances which tend to nourish the adult body, and to form and nourish the offspring, viz., the ovum, semen, and milk. No satisfactory formula has been suggested to express their chemical composition, but the average per-centage of the elements they contain is remarkably alike in all members of the group. This may be said to be in round numbers as follows :—

Oxygen	22 per cent.
Hydrogen	7 „
Nitrogen	16 „
Carbon	53 „
Sulphur	2 „

They are amorphous, of varying solubility, and with one exception indiffusible in distilled water.

As far as we know at present, albumins cannot be constructed *de novo* in the animal body, but must be supplied in one form or another as part of the food. Albumins are therefore always the outcome of the activity of vegetable life.

They can be recognised by the following tests :

1. Strong nitric acid gives a pale yellow colour to solutions or solid albumin especially on heating, which turns to deep orange when ammonia is added (*Xanthoproteic test*).
2. Millon's Re-agent (acid solution of proto-nitrate of mercury) gives a white precipitate which soon turns yellow, changing to rosy-red on boiling, or standing for some days.
3. Solution of caustic soda and a drop of copper sulphate solution give a violet colour to the liquid.
4. Acetic acid and boiling give a white precipitate, except with derived albumins and *peptones*.
5. Acetic acid and potassium ferro-cyanide give a flocculent white precipitate, except with *peptones*.
6. Acetic acid and equal volumes of sodium sulphate solution give a precipitate on boiling.
7. With sugar and sulphuric acid they become violet.
8. Crystals of picric acid added to solutions dissolve and cause bead-like local coagulations, except with *peptones*.

Classification of Albumins.

Under the head of the albuminous bodies we find several classes which differ from each other in slight but very important points. The first class may be called :—

A. *Albumins Proper, or Native Albumins.*

They consist of :

1. *Egg-Albumin*, which does not occur in the ordinary tissues of the animal, can be procured by filtration from the white of an egg. It makes a clear or slightly opalescent solution in water, from which it is precipitated by mercuric chloride, silver nitrate, lead acetate, and alcohol. It is coagulated by heat, strong nitric and hydrochloric acids, or prolonged exposure to alcohol or ether.

2. *Serum-Albumin*, on the other hand, is one of the chief forms of albumin found in the nutrient fluids.

It differs from egg-albumin in—

(*a.*) Not coagulating with ether.
(*b.*) The precipitate obtained by strong hydrochloric acid being readily redissolved by excess of the acid.
(*c.*) Coagulum being more readily soluble in nitric acid.
(*d.*) Its specific rotary power being 56°, while that of egg-albumin is 35·5°.

(*e.*) If introduced into the circulation, it is not eliminated with urine as is egg-albumin.

B. *Globulins.*

Associated with the last during the life of the tissues we find another class of albumins, namely, the globulins, which do not dissolve in pure water, but are more or less soluble in a solution of common salt. These may be divided as follows :—

1. *Globulin* (*crystallin*) occurs in many tissues, but is usually obtained from an extract of the crystalline lens made by triturating it with fine sand in a weak solution of common salt, and then passing a current of carbon dioxide through the solution. The globulin falls, being easily precipitable from its saline solution by very weak acid. This form of globulin does not cause coagulation when added to serous fluids, and in this respect differs from the next members of this division.

2. *Paraglobulin* (*serum-globulin*) can be obtained by passing through diluted serum a brisk stream of carbon dioxide. It is also precipitated by adding sodic chloride to saturation. When a fluid containing paraglobulin is added to a serous transudation, it causes coagulation of the fluid giving rise to fibrin.

3. *Fibrinogen*, a viscous precipitate got from serous fluids or blood-plasma in the same way as the last, but with greater dilution and more prolonged use of carbon dioxide. It is similar in its characters to the last, but coagulates at a lower temperature (55° C.) (paraglobulin coagulating at 60°—70° C.). On its addition to defibrinated blood, or a fluid containing paraglobulin, it forms a coagulum.

4. *Myosin* is obtained from dead muscle, being the soft jelly-like clot formed during *rigor mortis* from the dying muscle plasma. It is not so soluble as globulin, for it requires a stronger solution of salt (10%) to dissolve it, and is precipitated from its saline solution by solid salt or by dilution. It is coagulated at 60° C.

5. *Vitellin*, a white granular proteid obtained from the yolk of egg. It is very soluble in 10 per cent. saline solution, from which it can be precipitated by extreme dilution, but not by saturation with salt. It coagulates between 70° and 80° C.

C. *Derived Albumins* (*Albuminates*).

1. *Acid Albumin* (*syntonin*) can be made from any of the preceding by the slow action of a weak acid ; or by adding strong acetic or hydrochloric acids to native albumin, such as exists in white

of egg, and dissolving the jelly, thus formed, in water. It is only soluble in weak acids—exact neutralisation precipitating it. With the least excess of alkali the precipitate redissolves, changing into alkali-albumin.

If it be dissolved in weak acid it will not coagulate on boiling, but it coagulates and becomes incapable of re-solution if heated while precipitated by neutralisation.

2. *Alkali-Albumin.*—Similar to the last, but produced by the action of either weak alkalies on dilute solutions, or strong solution of potash on white of egg. Its general behaviour is the same as the above, but if prepared by strong solution of potash and allowed to stand some time it differs in composition, being deprived of its sulphur. It can then be distinguished by the absence of the brown coloration which appears on heating acid-albumin with caustic potash and lead acetate.

3. *Casein* is the proteid existing in milk, and resembles alkali-albumin in its reactions. It can be precipitated from milk by *rennet*, or acetic acid in excess, but not by exact neutralisation, owing to the presence of neutral potassium phosphate which must be converted into the acid salt before precipitation begins.

D. *Fibrin.*

A solid filamentous body, the result of chemical changes accompanying the death of the blood-plasma, during which the so-called fibrin generators are set free. It swells in weak hydrochloric acid, but does not dissolve while cold. If heated to 60° C. in acid, it changes to acid-albumin and dissolves. By 10 per cent. neutral saline solutions, a substance like a globulin may be extracted from it. If heated, it assumes the characters of a coagulated proteid.

E. *Coagulated Albumin.*

If any of the above be heated over 70° C. (except acid and alkali albumin, which must first be precipitated by neutralisation) they coagulate and become extremely insoluble and lose their former characters. They are but very slightly acted on by weak acids, even when warmed. Strong acids dissolve them, but this solution is associated with a destructive change. They are, however, converted by the digestive ferments and juices into peptones, and thus dissolved.

F. *Peptone.*

This substance is formed by the action of the digestive ferments from any of the above albumins, in the stomach by pepsin in the

presence of dilute acid, and in the small intestines by trypsin in the presence of dilute alkali. This change renders them more soluble and diffusible, and thus enables them to pass out of the alimentary canal into the system, and makes them more suited to take part in the nourishment of the body.

The leading characteristics of peptones may be thus enumerated :—

1. Very ready solubility in hot or cold water, acids or alkalies.
2. Not coagulable by heat.
3. They are precipitated by alcohol but not changed to the coagulated form.
4. They diffuse more readily through animal membrane than any other albumins.
5. They are not precipitated by copper sulphate, ferric chloride, or potassium ferro-cyanide and acetic acid.
6. They are precipitated by iodine, chlorine, tannin, mercuric chloride, and the nitrates of silver and mercury.
7. Caustic potash and a trace of copper sulphate added to their solutions give a red colour which deepens to violet if too much of the copper salt be used.

The formation of peptones is a gradual process having many intermediate steps, in the earlier stages of which, precipitates are formed by potassium ferro-cyanide and acetic acid. (*Vide* Chaps. VIII. and IX. on Chemistry of Digestion.)

Group III. Albuminoids.

These are the outcome of nutritive modification of protoplasm, and may be said to be directly manufactured by that substance, and to be specially adapted to meet the requirements of certain textures differing widely in function.

They are allied to one another and to the last group by—(a) their percentage composition* ; (b) containing nitrogen ; (c) being amorphous colloids.

---

* The following Table gives the composition of the principal albuminoids and albumin :—

	Gelatin.	Elastin.	Chondrin.	Mucin.	Keratin.	Albumin.
C	50 %	55 %	47 %	50 %	51 %	51—54 %
H	7	7	6	7	6	6—7
N	18	17	14	10	17	15—17
O	23	20	31	33	21	20—23
S	0·5		0·6		3	2—2·3

They differ from albuminous bodies in—(a) their solubility; (b) their behaviour to heat, acids, alkalies and the digestive fluids; and (c) their value as food-stuffs.

1. *Mucin* is the characteristic ingredient of the mucus manufactured by epithelial cells, and is also found in connective tissue (abundantly in that of the fœtus) and in some pathological growths. It gives a peculiar thick ropy consistence to the fluid containing it, enabling it to be drawn into threads. It is precipitated by mineral acids, alum and alcohol, and the precipitate swells in water and is re-dissolved in excess of the acid. With acetic acid a precipitate is formed which does not re-dissolve in excess of the acid. When boiled with sulphuric acid it yields leucin and tyrosin.

2. *Chondrin* is obtained by the prolonged boiling in water of slices of cartilage cleared of the perichondrium. On cooling, this solution forms a jelly. The jelly dissolves easily in hot water or alkalies, and can be precipitated by acetic or weak mineral acids, alum or acetate of lead. It gives only leucin on boiling with sulphuric acid.

3. *Gelatin* is produced by boiling fibrous connective tissues, such as ligaments, tendons, the true skin and bones in water. On cooling, the fluid forms a jelly, which can be dried to a colourless brittle body which swells in cold water and dissolves on being heated. It is not precipitated by acetic acid, but yields precipitates with mercuric chloride or with tannin, as seen in making leather. On boiling with sulphuric acid it yields glycin and leucin but no tyrosin.

4. *Elastin* is obtained from yellow elastic tissue by boiling with caustic alkalies. It is little affected by boiling water, strong acetic acid, or weak alkalies, but dissolves in concentrated sulphuric acid. It is precipitated by tannin, and yields leucin when boiled with sulphuric acid.

5. *Keratin* exists in the epidermic appendages (hair, horn, nails, &c.). It resembles the albuminous bodies in containing a considerable quantity of sulphur, but differs from them and the other albuminoids in general properties. It is soluble in alkalies, swells in strong acetic acid, gives the xanthoproteic reaction, and is insoluble in the digestive juices.

Group IV. Products of Tissue Change.

Intermediate or bye products.

These are protoplasmic manufactures destined for some useful purpose, but they do not long exist in their original form; being

often broken up into other compounds, they are re-absorbed, or pass away with the fæces. These bodies are found in the various secretions. Most of them can be better described with the function of the gland which forms the secretion in which they occur.

Attention must here be drawn to certain complex bodies existing in the bile. Some complex nitrogenous substances and the monatomic alcohol, cholesterin, will now also be mentioned. But the reader must remember that chemically they are not connected with the other bodies the description of which immediately follows theirs, namely the effete products.

Bile Salts.—Two acids exist in the bile united with soda to form soluble soap-like salts. They may be recognised by the purple violet colour produced by cane-sugar and sulphuric acid at a temperature of about 70° C. (Pettenkofer's reaction).

Taurocholic Acid, $C_{26}H_{45}NSO_7$, is most plentiful in the bile of carnivora, where it occurs combined with soda. It is decomposed by prolonged boiling with water into taurin and cholic acid, thus :—

$$\underset{\text{Taurocholic Acid.}}{C_{26}H_{45}NSO_7} + H_2O = \underset{\text{Taurin.}}{C_2H_7NSO_3} + \underset{\text{Cholic Acid.}}{C_{24}H_{40}O_5}.$$

Glycocholic Acid, $C_{26}H_{45}NO_6$, found in the bile of herbivora and man. It crystallises in fine white glistening needles. It exists as the glycocholate of soda in the bile. By boiling with weak acid, it yields glycin and cholic acid.

$$\underset{\text{Glycocholic Acid.}}{C_{26}H_{45}NO_6} + H_2O = \underset{\text{Glycin.}}{C_2H_5NO_2} + \underset{\text{Cholic Acid.}}{C_{24}H_{40}O_5}.$$

In the bile certain matters also exist to which the colour is due, the principal being *bilirubin* in man and carnivora, and *biliverdin* in herbivora. They are probably derived from the colouring matter of the blood. They can be recognised by treating the solution with nitric acid which is coloured with red fumes, when a play of colours is seen passing through stages of green, blue, violet, red, and yellow.

Lecithin, $C_{44}H_{90}NPO_9$, is a complex nitrogenous fat found in most tissues and fluids of the body, particularly in the nerve tissues and yolk of egg. It is an interesting product of decomposition of the constituents of the brain, and is related in constitution to the neutral fats ; it may be regarded as an acid glycerine ether. It is easily decomposed when heated with baryta water, splitting into glycerin-phosphoric acid, neurin, and barium stearate.

Another body called *Cerebrin*, not containing any phosphorus and of doubtful composition, can be obtained from brain substance, and is also found in nerve fibres and pus corpuscles. It is a light colourless powder which swells in water.

Protagon, $C_{160}H_{308}N_5PO_{35}$, is by some supposed to be the chief constituent of brain substance, and by others a mixture of the last two bodies.

Neurin (*Cholin*), $C_5H_{15}NO_2$, is an oily liquid only found in the body as a product of the decomposition of lecithin, but it has been obtained synthetically.

Cholesterin, $C_{26}H_{44}O+H_2O$, exists throughout the body where active tissue change is going on, particularly the nervous centres. It is a monatomic alcohol, and is the only one existing free in the body. It may be obtained from gall-stones, some of which consist entirely of cholesterin. It may occasionally be found in a crystallised form in many of the fluids of the body but never in the tears or urine, and only seems to be an effete product, nearly all that produced in the body being discharged with the effete portions of the bile. It may be recognised by the shape of the crystals formed from a solution in alcohol, which are rhombic plates, in which one corner is generally deficient.

Effete Products.

These, as has been stated before, are generally the outcome of the active chemical changes necessary for the growth and vitality of the living protoplasm, and are for the most part soon eliminated by the excretory glands, so that but small quantities of them can be found in the active tissues where they are produced.

Urea, $CO(NH_2)_2$, is the most important constituent of the urine of mammalia, but not of that of birds or reptiles. Traces of it may be found in the fluids and tissues of the body. It is readily soluble in water and alcohol, and forms crystals when its solution is concentrated. It decomposes when treated with some strong acids or alkalies, taking up water and yielding CO_2 and NH_3; and with nitrous acid gives $CO_2 + N_2 + 2(H_2O)$. It was the first of the so-called "organic" compounds to be made artificially, being obtained by Wöhler in 1828 by mixing watery solutions of potassium cyanate and ammonium sulphate, evaporating to dryness and extracting with alcohol, or in short by heating ammonium cyanate with which it is isomeric.

Ammonium Cyanate.		Urea.
$NH_4 \cdot CNO$	=	$CO \cdot NH_2 \cdot NH_2$.

It can now be produced artificially in other ways.

It has also been considered a *monamide of carbamic acid* ($CO{\cdot}OH{\cdot}NH_2$) a molecule of hydroxyl being replaced by one of amidogen, NH_2, thus—$CO{\cdot}NH_2{\cdot}NH_2$. In the presence of septic agencies, in a watery solution, urea takes up two molecules of water and is converted into ammonium carbonate—

$$CO(NH_2)_2 + 2H_2O = CO(ONH_4)_2.$$

The so-called alkaline fermentation of urine depends upon this change. The reader is referred to the Chapter on Excretions, p. 329, where more complete information is given.

Kreatin, $C_4H_9N_3O_2$, occurs in muscle and many other textures. It may be converted into kreatinin by the action of acids by simple dehydration. It can also be split up into sarcosin and urea.

Kreatinin, $C_4H_7N_3O$, is a dehydrated form of kreatin, which is a normal constituent of urine. In watery solutions it is slowly converted into kreatin.

Allantoin, $C_4H_6N_4O_3$, found in the allantoic fluid and the urine of the fœtus and pregnant women. It is crystallisable, and is converted into urea and allantoic acid by oxidation.

Glycin (*Glycocoll* or *Glycocine*) $C_2H_2(NH_2)O{\cdot}OH$, is regarded as amido-acetic acid. It does not occur free in the body, but enters into the composition of the bile acids and hippuric acid. It is soluble in water, and insoluble in cold alcohol and in ether.

Leucin, $C_6H_{10}(NH_2)O{\cdot}OH$, or amido-caproic acid, is found in the secretion of the pancreas and some other glands. It is one of the principal products of the decomposition of albuminous bodies, from which it can be obtained by boiling with sulphuric acid, in the form of peculiar rounded crystals.

Tyrosin, $C_9H_{11}NO_3$, though belonging to a distinct chemical series (aromatic), is only found in company with leucin in the decomposition of albuminous bodies, and normally in the pancreatic secretion. Its constitution is said to give warranty for the name oxy-phenyl-amido-propionic acid.

Taurin, $C_2H_7NSO_3$, is a constituent of one of the bile acids, and is also found in muscle-juice. It may be regarded as amido-ethyl-sulphonic acid.

Uric Acid, $C_5H_4N_4O_3$ (dibasic), is found in large quantities in the excrement of birds and reptiles, but in a small and variable quantity in the urine of man. Traces have been found in many tissues, in some of which quantities accumulate as the result of pathological processes (gout). It forms salts which are much less soluble in cold than in hot water, and make the common sediment in urine. The

acid salts are less soluble than the neutral. The common test for uric acid consists of slowly evaporating the substance to dryness with a little nitric acid, and to the residue adding ammonia, when a bright purple colour is produced (murexide test). Uric acid is supposed to be a step in the production of urea, which is one of the results of its oxidation in the presence of acids, thus :—

Uric Acid. Alloxan. Urea.

$$C_5H_4N_4O_3 + H_2O + O = C_4H_2N_2O_4 + CO(NH_2)_2.$$

Hippuric Acid, $C_9H_9NO_3$, occurs in considerable quantities in the urine of the horse and herbivora generally. It is found but very sparingly in man's urine, but it appears in large quantities after benzoic acid and some other medicaments have been taken. In constitution it is an amido-acetic acid in which one atom of the hydrogen is replaced by the radical benzoyl (C_7H_5O). In the body it is combined with bases, and is formed out of benzoic acid and glycin (amido-acetic acid), thus—

Glycin. Benzoic Acid. Hippuric Acid. Water.

$$C_2H_2(NH_2)O\cdot OH + C_7H_6O_2 = C_2H(C_7H_5O)(NH_2)O\cdot OH + H_2O.$$

By heating or putrefaction it is resolved into these constituents.

Indol, C_8H_7N, is produced in the intestinal canal by the putrefactive changes brought about by septic agencies during pancreatic digestion. It gives an odour to the fæces and a red colour with nitrous acid.

Indican, a peculiar substance sometimes found in the urine and sweat. With oxidising agents it yields indigo blue. By this fact it is easily recognised. An equal volume of hydrochloric acid and a very small quantity of calcium hypochlorite (bleaching-lime) is added, and the indigo which is formed can then be dissolved and separated by agitation with chloroform.

Class B. NON-NITROGENOUS.

Group V. Carbohydrates.

Carbohydrates (general formula, $C_mH_{2n}O_n$) are bodies in which the hydrogen and oxygen exist in the same proportion as in water, the carbon being variable. The following examples of this group are met with in the textures of the body :—

Grape-Sugar (*Dextrose*), $C_6H_{12}O_6$, occurs in minute quantities in the blood, chyle, and lymph. It forms crystals which readily dissolve in their own weight of water. The watery solution has a

dextro-rotatory power on the ray of polarised light. When mixed with yeast, the fungus (*Saccharomyces cerevisiæ*) of the yeast causes *alcoholic fermentation* of the sugar, whereby alcohol and carbon-dioxide are formed.

$$\overset{\text{Dextrose.}}{C_6H_{12}O_6} = 2\,\overset{\text{Alcohol.}}{C_2H_6O} + 2\,CO_2.$$

Moderate heat (25° C.) aids the process, and cold below 5° C. checks it ; an excess of either sugar or alcohol stops it.

The presence of casein or other proteid material, when decomposing, gives rise to *lactic fermentation*, producing first lactic acid, then butyric acid, carbon-dioxide and hydrogen.

$$\overset{\text{Dextrose.}}{C_6H_{12}O_6} = 2\,\overset{\text{Lactic Acid.}}{C_3H_6O_3} = \overset{\text{Butyric Acid.}}{C_4H_8O_2} + 2\,CO_2 + H_4.$$

Milk Sugar (*Lactose*), $C_{12}H_{22}O_{11} + H_2O$, metameric with cane-sugar (sucrose).—It is the characteristic sugar found in milk. It is not so soluble as dextrose, and does not undergo direct alcoholic fermentation, but under the influence of certain organisms it readily gives rise to lactic acid by lactic fermentation in the same way as dextrose. (See page 70.)

Inosit, $C_6H_{12}O_6 + 2\,H_2O$, is an isomer of grape-sugar, which is incapable of undergoing alcoholic fermentation. It is crystallisable, and easily soluble in water. It has no effect on the polarised ray. It is found in the muscles, and also in the lungs, spleen, liver, and brain.

Glycogen, $C_6H_{10}O_5$, a body like dextrin, first found in the liver. It gives an opalescent solution in water, and is readily converted into dextrose by an amylolytic ferment, or weak acids. It has a strong dextro-rotatory power. It can be found in most rapidly growing tissues. (See Glycogenic Function of the Liver.)

Group VI. Fats.

These bodies have the same elements in their composition, but the hydrogen and oxygen have variable proportions—not that of water. Fats are found in large masses in some tissues, and also as fine particles suspended in many of the fluids. The fat of adipose tissue in man is a mixture of olein, palmitin, and stearin, which are spoken of as the neutral fats.

The first is liquid and the last two solid at normal temperatures

and the varying consistence of the fat of different animals depends upon the relative proportions of the solid or liquid fats.

Fats are soluble in ether and chloroform, but quite insoluble in water. When agitated in water containing an albuminous body, and an alkaline carbonate in solution, fluid fat is broken up into small particles, which remain suspended in the liquid, forming an opaque milky emulsion.

Chemically, they are regarded as ethers derived from the triatomic alcohol glycerine, $C_3H_5(OH)_3$, by replacing the OH group with the radicals of the fatty acids: thus—

Glycerine + Palmitic Acid = Tripalmitin + Water.

$$C_3H_5(OH)_3 + 3\,(C_{16}H_{32}O_2) = C_3H_5\,(C_{16}H_{31}O_2)_3 + 3\,H_2O.$$

Under the influence of certain ferments they separate into glycerine and the fatty acid, uniting with the necessary elements of water.

When the neutral fats are boiled with alkaline solutions they are similarly decomposed, and uniting with the elements of water, form glycerine and fatty acids. The glycerine is thus set free, but the fatty acid combines with the alkaline metal to form a soluble *soap*. An insoluble soap may be obtained by substituting lead or lime, &c., for the alkali.

This splitting up of the neutral fats, stearin, palmitin, and olein into sodium stearate, palmitate, or oleate goes on during digestion and is said to be useful in aiding the absorption of fatty matters.

INORGANIC BODIES.

Water (H_2O) is present in nearly all tissues in larger proportion than any other compound, making up about 70 per cent. of the entire body-weight. The amount in each texture varies, the different tissues having widely different consistence.

Water is introduced into the body not only as drink, but a large quantity is also taken with our solid food. It is highly probable, that in the chemical changes which take place in the tissues, some water is formed by the oxidisation of the hydrogen of the more complex substances.

In the economy it acts as the universal solvent in the fluids of the body, and as the agent by means of which the chemical changes of the various organs can be accomplished.

Water leaves the body by the lungs as vapour, and by the skin, kidney, and many other glands, as the fluid in which the solids of their secretions are dissolved.

Inorganic acids occur in the body, either combined, forming salts in which condition we find several (sulphuric, phosphoric, silicic), or uncombined. In the latter state we have only two, viz :—

Hydrochloric Acid, HCl, which is formed in the stomach, and plays an important part in gastric digestion.

Carbonic Acid Gas, CO_2, exists in most of the fluids of the body, having been absorbed by them from the tissues. The venous blood contains a considerable quantity, some of which is got rid of during the passage of the blood through the lungs. It is a waste product, which must be constantly eliminated from the body (see Respiration).

Salts. A large number of salts occur in the tissues, generally in small quantity, in solution. In the teeth and in bone-tissue salts exist in the solid form, and in much greater proportion than in any of the soft parts. Most of the salts are introduced into the economy with the food, but some, doubtless, are formed in the body itself. Our knowledge of the exact position occupied by the salts in the textures is very incomplete, as their amount is usually estimated from the ash of the tissue which remains after ignition, by which process some become altered, so that it is impossible to say what are the exact salts that are present in the body. They form chemical combinations with the complex organic compounds, which we do not understand, and probably have important functions to perform, such as rendering certain materials (globulins) soluble, or otherwise facilitating tissue change. The salts pass out of the body in many secretions, largely in the urine, where they influence the elimination of urea, and therefore form an important constituent of that secretion.

Common Salt (*Sodium Chloride*), NaCl, is the most widely distributed, and is present in greater quantity than any other salt in all animal fluids and most tissues, except bones, teeth, red blood corpuscles, and red muscle.

Potassium Chloride commonly accompanies sodium chloride in small quantity. In the red blood corpuscles and in muscle it occurs in greater amount than the sodium salt, while in the blood plasma but little is found in comparison with the sodium salts, and any excess seems to act as a poison to the heart.

Carbonates and phosphates of calcium, sodium, potassium, and magnesium occur in small quantities in most tissues. The earthy part of bone is chiefly composed of calcium and magnesium phosphate and calcium carbonate, together with some calcium fluoride.

Sulphates of sodium and potassium, probably formed in the body

from the oxidisation of the sulphur in the complex proteid materials, occur in most tissues, and are removed from the body by the kidneys.

Finally we find two of the elements free in the textures. Of these *Oxygen* plays by far the most important part. It is widely distributed among the fluids of the body, from which it can be removed by reducing the pressure of oxygen of the atmosphere by means of an air-pump. Oxygen is introduced into the body by the lungs, where the blood takes it from the air. In the blood only a small quantity of that which can be removed by the air-pump is really free; the remainder is chemically combined with the colouring matter of the blood. It is absolutely necessary for life, as it alone can enable the chemical changes of the tissues, which are mostly oxidisations, to go on. It is, in fact, the element necessary for the slow combustion which takes place in the nutrient material after its assimilation.

Nitrogen also occurs in the blood, but in insignificant quantity. It is absorbed from the atmosphere as the blood passes through the lungs. So far as we know, it has no physiological importance in the body.

CHAPTER IV.

THE VITAL CHARACTERS OF ORGANISMS.

THE manifestation of so-called *vital phenomena* in man forms the subject-matter of the following chapters, and some explanatory definition of the vital characters of the simpler organisms will be useful in preparing the beginner's mind for the more intricate questions in human physiology. This, with the foregoing short account of the chemical and structural peculiarities of animals, will complete a rough outline of the general character of organisms.

Protoplasm has already been referred to as the material capable of showing vital phenomena, the most obvious and striking of which are its movements.

Besides the common molecular or Brownian movement of the granules in protoplasm—which may be seen in most cases where fine granules are suspended in a less dense medium—protoplasm can perform motions of different kinds which must be regarded as distinctly vital in character. This movement may be said to be of three different kinds, according to the results produced, viz. :—(1.) The production of internal currents. (2.) Changes in form. (3.) Locomotion. In reality the two latter are dependent on the first.

The existence of *currents* moving from one part of the protoplasm to another can be well seen in vegetable cells, when the cell-wall restricts the more obvious change in form or place. Thus in the cells forming the hair on the stamens of *Tradescantia Virginica* the various currents can be seen in the layers of protoplasm which line the cell-wall.

The granular particles course along in varying but definite directions, passing one another like foot-passengers in a crowded street. The first and most obvious result of this is, that the different parts of the substance are frequently brought into contact with one another, and thus the products of any chemical changes taking place at a given part of the cell-body are rapidly distributed over the entire mass of the protoplasm.

The *change in form* occurs if there be no definite cell-wall—as in naked vegetable spores and amœboid forms of animal life—to restrict or direct the current of protoplasm ; it flows out in various directions in bud-like processes, which appear at various parts of the protoplasmic mass, so as to cause a constant change in the form of the cell. These outstretched processes sometimes flow together and become fused, often enclosing some of the medium in which the creature is suspended, or catching some foreign particle floating near them.

The flowing out of these *pseudopodia* usually takes place for some time persistently from one side of the cell ; and the body of the cell has to follow, as it were, the protrusion of the processes in such a manner that in a short time definite change in position or movement in a certain direction occurs : thus the protoplasmic unit may be said to perform definite progression or *locomotion*. All these movements may be seen in the white blood corpuscle of a cold-blooded animal, such as a frog, and still more easily in the unicellular amœba.

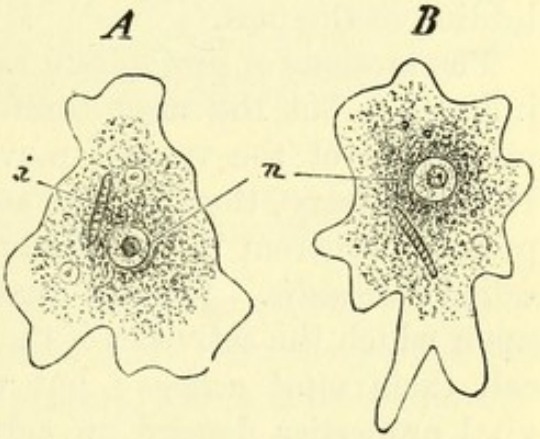


Fig. 35.—An amœba figured at two different moments during movement, showing a clear outer layer and a more granular central portion. (*n*) Nucleus; (*i*) Ingested food. (Gegenbauer.)

Various influences may be seen to affect the rate of movements and probably influence at the same time the other activities of the protoplasm. Foremost among these must be named :—(1.) *Temperature.* If a protoplasmic unit, which is observed to be motile, be gently warmed, the movements become more and more active as the temperature is raised, up to a certain point, about 35°—42° C., when a spasm occurs, resulting in the withdrawal of the pseudopodia ; soon after this the cell assumes a spherical shape. If the heat be carefully abstracted before it has attained too great a height, the protoplasm may recover and again commence its movements. If, on the other hand, cold be applied to moving protoplasm, the motions become less and less active, and commonly cease at a temperature about or a little above 0° C. (2.) *Mechanical irritation* also produces a marked effect on the movements of protoplasm. This may be well seen in the behaviour of a living white cell of frog's blood under the microscope. It is spherical when first mounted, owing to

the rough treatment it goes through while being placed on the glass slide and covered ; shortly its movements become obvious by its change in form, which may again be checked by a sudden motion of the cover-glass. (3.) *Electric shocks* given by means of a rapidly-broken induced current cause spasm of the protoplasm, the cell becoming spherical. (4.) *Chemical stimuli* also have a marked effect ; carbonic acid causing the movements to cease, and a supply of oxygen making it active. The movements and other activities of protoplasm are, during life, frequently modified and controlled by nerve influence, as will appear in the following pages. This may readily be seen in the stellate pigment cells of the frog's skin, which can be made to contract into spheres by the stimulation of the nerves leading to the part.

The motions of protoplasm are thus seen to be affected by external influences, but the most careful observer cannot find physical explanations of the various movements which have been described. It is necessary, therefore, to ascribe this power of motion to some property inherent in the protoplasm, and hence the movements are called *automatic.* We are unable to follow the chemical processes upon which the activities of the protoplasm depend, and we therefore call them *vital actions ;* but we must assume that these so-called vital properties depend on certain decompositions in the chemical constitution of the protoplasm. We know that some chemical changes take place, as we can find and estimate products which indicate a kind of combustion ; but we know little or nothing of the details of the chemical process.

From the foregoing description of the manner in which protoplasm responds to external stimuli, it may be gathered that it is capable of appreciating impressions from without ; indeed it can be said *to feel.* We can only judge of the sensitiveness of any creature by the manner in which it responds to stimuli, and we may therefore conclude that the smallest particle of living protoplasm is endowed with definite sensitiveness : this must be noted as one of the most striking properties of protoplasm.

Every particle of living protoplasm has the power of *assimilation.* Taking into its structure any nutrient matters it meets with, by flowing around them in the way mentioned, it brings them into direct contact with different parts of its protoplasmic substance. This nutrition of the cells gives rise to their growth, and finally leads to their reproduction. These facts will be more closely examined when speaking of their relation to cell life.

When a certain size has been attained, the cell does not further

increase, but prepares to bring forth a cell unit similar to itself. This is spoken of as the *reproduction* of cells.

Different kinds of cell-reproduction have been observed, which are all, however, modifications of the same general plan. The first is

Fig. 36.—Cells of the yeast-plant in process of budding, between which are some bacteria.

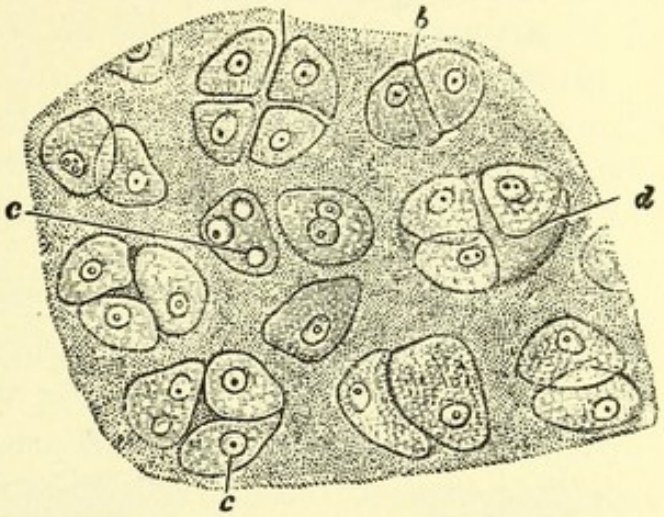


Fig. 37.—Cartilage from young animal showing the division of the cells (*a*, *b*, *c*, *d*).

that by the formation of a *bud* from the side of the parent cell ; this bud increases in size, and finally detaches itself from the parent and becomes a separate individual. This process, which is called *gemmation*, can readily be seen in all its stages in growing yeast, where the torula cells have various-sized buds growing from them. If the newly-formed portion be large, nearly equal in size to the cell itself, the process receives the name of *fission*, or division. In well-marked typical fission the parent cell divides into two parts of equal size, each of which becomes a perfect individual. Various gradations may be traced between the two processes, so that it is difficult to draw any very distinct line between budding and fission. The budding and fission may be multiple ; many buds and several units, products of division, may remain together, and form what is called a colony. When this multiple budding or division takes place, so that the new units are included within the body of the parent cell, then the process is called *endogenous reproduction* or spore-formation. Just as there are gradations between budding and fission, so it is difficult

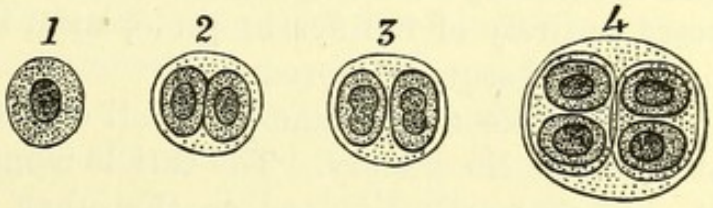


Fig. 38.—Cells of a fungus (*Glæocapsa*) showing different stage (1—4) of endogenous division. (After Sachs.)

to draw a hard and fast line between what may be called multiple fission and spore-formation.

In tracing the stages of development of the highly differentiated cells of some tissues, we have to pass through a series of changes which form a cycle that may well be called the life-time of the cell.

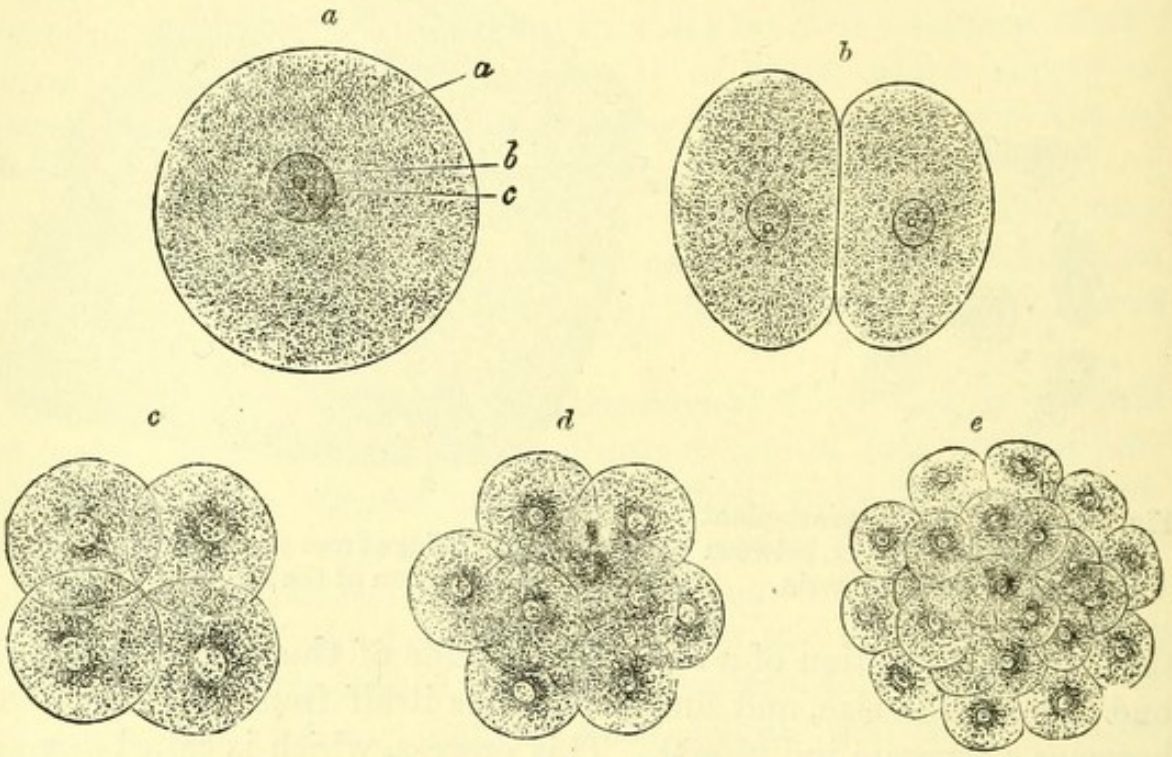


Fig. 39.—Division of egg-cell. (Gegenbauer.)

The duration of this cycle varies greatly in different individual cells. Some cells are very short-lived, being destroyed by their act of secretion; others probably endure for the life-time of the animal. The life-history of all cells begins with the stage when they are composed entirely of indifferent protoplasm, in which various modifications are subsequently produced.

Let us take as an example a cell of the outer skin or *cuticle*, and examine its life-history. The cuticle is made up of numerous layers of epithelial cells laid one on the other, and the surface cells are constantly being rubbed or worn off. These cells have their origin from the cells of the deepest layer, which is next to the supply of nutriment. This layer is made of soft protoplasmic units, which have, no doubt, certain specific inherited characteristics, but apparently the same as the motile, sentient, growing protoplasm of an indifferent cell. By a process of fission or budding, constantly going on in this deepest layer of cells, new protoplasmic units are produced. These become distinct individuals, and occupy the position of the parent cell, which having produced offspring, is moved one place nearer the surface, away from the supply of

food. The new cell in time gives rise to offspring, and having attained reproductive maturity, in turn is moved onward to the surface. The result of this is that its supply of nutrition diminishes, the evidences of reproductive activity disappear, and at a certain point all signs of protoplasmic life are lost. But on its way from the seat of its origin to the surface, it makes use of its limited supply of nutrition for the purpose of manufacturing a special kind of material which, if present at all, only occurs in the minutest traces in ordinary protoplasm. As the cell moves towards the surface, it loses its protoplasmic characters, becomes tougher and drier, and finally nothing but the special horny material remains. Thus from the birth of the cell, its energies are devoted, first to its own growth, then to the reproduction of its like, and finally to the formation of a material fitted to act as a mechanical protection to the surface of the skin. Having manufactured a certain amount of this material, the protoplasm dwindles, and finally disappears, so that the cell may be said to die. Its horny insoluble and impermeable skeleton has, however, yet to do service in the outer layer of the skin while it is passing towards the surface, to be in its turn rubbed off.

It has already been stated that the material protoplasm, which forms all active cells, is capable of carrying on the many functions required for the independent existence of simple creatures. It will be found in the subsequent pages that, not only can protoplasm perform all the activities necessary for the life-history of unicellular organisms, but that it can also work out all the functions of the most complex animals. Indeed, the cells which accomplish the most elaborate functions in man, are but protoplasm more or less modified for the special purpose to be attained.

The different living operations of many independent unicellular organisms can be more completely watched than the changes which take place in the cells of the higher animals, both on account of their greater size, their freedom, and the more obvious character of the changes taking place in them. The student is therefore advised to spend some time in contemplating the operations which go on in those simple organisms, whose life is not complicated by structural or functional elaboration, before attempting to solve the difficult question of the mechanism of the human body.

The lowest forms of living creatures that we are acquainted with (*micrococcus* and *bacterium*), are placed among the fungi in the vegetable kingdom. On account of their extremely minute size—being

hardly visible as spherical or elongated specks with a powerful microscope—we can say but little about their structure. They appear to be translucent and homogeneous.

Since we use the term protoplasm to denote the material of which the active part of the simplest forms of living beings are composed, we must assume that bacteria are small particles of that material, but the characters attributed to protoplasm cannot be detected in the minute glistening mass which makes up their body.

They are so certain to appear in a couple of days in organic infusions, or in any fluid prone to putrefaction, and multiply with such astounding rapidity, that they have been supposed by some to develop spontaneously. But this is now known not to be a fact. Bacteria can no more than any other form of living thing appear without progenitors. They float inanimate and dry in multitudes through our atmosphere, and adhere to all substances to which the air has free access. The moment they light upon a suitable habitat, they burst into prodigious activity, at first forming masses or colonies, which may be seen as a jelly-like scum on the fluid. Such a habitat is supplied by any organic substance capable of ready decomposition, for which process, as is well known, the great requirements for life, moisture and warmth, are to a certain degree necessary. Vast varieties of these organisms are now known. They differ slightly in shape, in their habitat, and in their properties. Some are obviously composed of two distinct layers, some are provided with a fine hair-like process, by the lash-like motions of which they move rapidly in a definite direction.

They are known to be inseparable from putrefactive changes in organic materials, without them no putrefaction can go on, since this process is but the product of their living activity. Great heat kills them, too great cold or dryness checks their activity and stops putrefaction. When an organic substance is absolutely protected from their presence by exclusion of the air, &c., no putrefaction occurs, even though it be prone to spontaneous decomposition, and be placed under favourable circumstances as to warmth and moisture.

Bacteria would not deserve so much notice here were it not for the pathogenic influence some of them have on the higher forms of life. We do not know that they are necessary for any of the more important processes that normally go on in the human body, though they are constantly present in the intestinal tract, and are inseparable from at least one change taking place there that may be regarded as physiological. It is their relation to the diseased state

that makes a knowledge of these creatures imperative to medical men.

So long as the tissue of a higher animal is healthy and well nourished, the commoner forms of septic bacteria cannot thrive in immediate contact with it. They can only exist in the intestine, &c., because there they find accumulations of lifeless fluids which offer them a suitable nidus. Active living tissues may be said to have antiseptic power, *i.e.* are able to destroy septic bacteria, and it is only owing to this bactericide power of our textures, that we can with immunity breathe into our lungs the atmospheric air often crowded with these organisms, and swallow multitudes of them with our food. But for it every wound would become putrid, every breath might admit deadly germs to our blood.

When the vitality of the body generally is lowered, the vital activity of the tissue may fall below that necessary to insure the death of the bacteria, whose victory is signalled by unwonted and often fatal changes. Morbid fluids allowed to accumulate in the textures facilitate the growth of bacteria, and give rise to various grades of "wound-infection." But if all accumulations be avoided, the bacteria brought into relation with the living tissue only irritate it, and cause general fever and local suffering to the patient. They cannot propagate in live tissue as in lifeless fluids. As a rule, the injurious effect of bacteria is in inverse proportion to the vital power of the textures which they invade. This is seen in many cases familiar to the physician and the surgeon. There are, however, many forms of *pathogenic* bacteria which, if introduced into the system by inoculation, are able to overcome the vital activity of the tissues of certain animals even in the most robust health.

We next come to forms of fungus, which set up a process very like putrefaction, such as the yeast-plant, *Torula cerevisia*, which causes alcoholic fermentation in sugar solutions. In the torula an external case containing protoplasm may readily be seen, and multiplication of the cells goes on rapidly by a process of budding. Torulæ, however, like bacteria, though called vegetables, have not the power of assimilating as ordinary green plants do, but require nutriment to be supplied to them which already contains organic or complex compounds. Structurally but little different from torula is a one-celled plant, the green protococcus, which, like a higher plant, can build up its texture from the simplest food-stuffs, and carry on its functions. It consists of a case made of cellulose, within which lies a mass of protoplasm with a nucleus. Their protoplasm is coloured green by a peculiar substance called chlorophyll. We shall see pre-

sently that it is to protoplasm containing chlorophyll, that plants owe all their most characteristic and wonderful properties ; viz., the property of assimilating so as to construct complex carbon compounds out of simple inorganic materials.

The smallest and simplest organisms classed as animals are generally larger than the vegetable cells just alluded to. They consist of protoplasm without any nucleus, and only sometimes with a structural difference between any part of their substance. As an example we may take *Protamœba*. This is a small mass of protoplasm without any nucleus, but its outer layer is clearer and less granular than the central part. It can move by sending out protoplasmic processes, in which currents can be observed resembling those in the vegetable

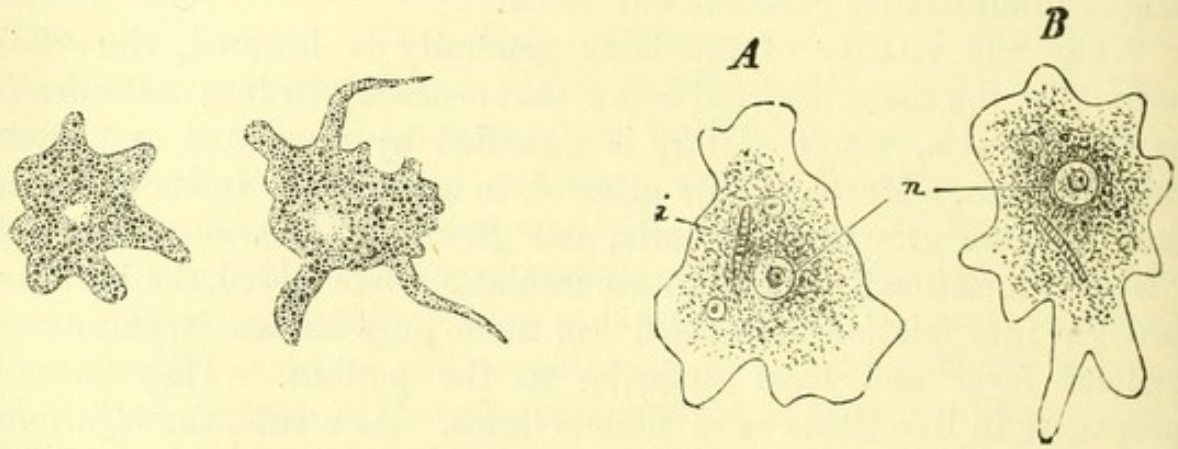


Fig. 40.—Two different forms of Amœbæ in different phases of movement. Those on the left after Cadiat. A and B show an outer clear zone. (Gegenbauer.)

cells. Excepting as regards the nucleus, it is much the same as the *Amœba*, which can be readily found and watched, and will be more accurately described.

The amœba is a single cell or mass of uncovered protoplasm, containing a well-defined nucleus, within which is a nucleolus. There is also generally a vacuole. The central part of the protoplasm is densely packed with coarse granules, but the outer more active part is structureless, and translucent-looking, somewhat like a fine border of muffed glass, encasing the coarsely granular middle portion. Such an animal has no parts differentiated for special purposes, the requirements of its functions being so limited that the protoplasm itself can accomplish them.

Thus the processes of protoplasm, which flow out with considerable rapidity from the body, frequently encircle particles of nutrient material, and then closing in around them, press them into the midst of the granular central mass. Here they sojourn some time, and during this period no doubt any nutritive properties they

possess are extracted from them, and they are then ejected from the plastic substance. This form of assimilation demands no previous preparation of the food such as we shall see takes place in the alimentary tract of man, and in the special organs of the higher animals ; yet it is a form of digestion adequate at least to the requirements of this simple organism. The repeated alteration of relationship between the different parts of the protoplasm, and the surrounding medium during the flowing hither and thither of the currents, produces not only a change in the shape and position of the animal, but also acts as a means of distributing the nutriment to the different parts of the body, and of collecting and carrying to the surface the various products of tissue-decomposition ; thus the streaming protoplasm does the work of a circulating fluid such as we see in the more elaborate organisms for the distribution of nutriment and elimination of waste materials. The surface of the amœba is sufficient to allow of the gas-interchange necessary for life, and by means of the ever-changing material exposed, sufficient oxygen is taken for its tissue combustions, and so a function of respiration is established. The growth that results from the perfect performance of these vegetative functions proceeds until the maximum size is attained, and further nutritive activity is then devoted to reproduction. When growth ceases, commonly the cell divides and forms two distinct individuals. The movements which form the most striking operations of the amœba are the same as those which take place in protoplasm except that they are more rapid and obvious. The clear outer layer first flows out as a bud-like process, and, as it is gradually enlarging, some of the central granular part of the cell suddenly tumbles into its midst, where it remains, while other pseudopodia are being thrown out in the neighbourhood, and the same changes repeated in them. It is difficult to watch the motions of an amœba without being impressed with the idea that it is not only endowed with sensibility but that it can also discriminate between different objects, for we see it greedily flowing around some food-material, whilst it carefully avoids other substances with which it comes in contact.

If a glass vessel, containing several amœbæ, be placed in a window, they will be found to cluster on the side of the glass most exposed to the light. From this it would appear that, in some obscure way, protoplasm can appreciate light, and respond to its influence by moving towards it.

This single-celled animal, or nucleated mass of protoplasm, can perform all the functions of a higher animal. It can move from

place to place and assimilate nutriment, apparently discriminating between different materials. It distributes nutrient stuffs and oxygen throughout its body by a kind of tissue circulation, and it can appreciate and respond to the most delicate form of stimulus, namely light, which subtle motion has no effect on the sensory nerve-fibres of the higher animals.

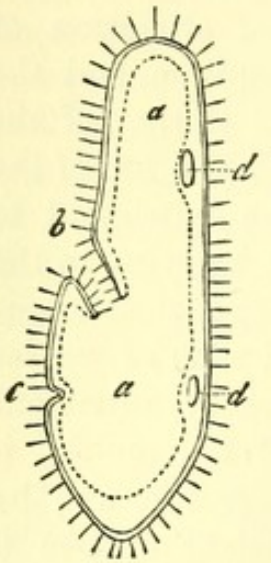


Fig. 41. — Diagram of Paramœcium showing digestive cavity. (*a a*) Body-space filled with soft protoplasm, into which food is taken. (*b*) Mouth. (*c*) Anus. (*d*) Contractile vesicle. (After Lachmann.)

In some unicellular animals certain parts of the cell are specially modified for the performance of special functions, a division of labour thus taking place which insures the more perfect accomplishment of the different kinds of activity. In one of the commonest of the Infusoria (*Paramœcia bursaria*), which swarm in dirty water, this is well exemplified. The outer layer of the flattened body is denser, and forms a kind of fibrillated corticular case (ectosarc), which is covered over with hair-like processes (vibratile cilia), constantly moving in a certain direction, so as to propel the creature rapidly through the water. The internal part of the cell is very soft, almost fluid, and coarsely granular in appearance, containing many bodies which have obviously been introduced from without. This soft internal protoplasm (endosarc) moves slowly round in a definite direction, completing its circuit in one or two minutes, and thus carries on a circulation which mixes the various matters contained in it. At one point of the ectosarc, or cortical layer, an orifice or mouth leading to an œsophageal depression is found. This orifice is lined by moving cilia, which by their vibrations drive the food into the œsophagus, whence it is periodically jerked into the soft internal protoplasm or endosarc, together with some water, and thus forms a food vacuole, which is carried round in the circulation of the ectosarc. Besides a well-marked nucleus and nucleolus in the central part of the cell, these paramœcia have one or more clear spaces placed near the surface at the extremities of the animal. These vacuoles suddenly contract, and disappear every now and then. When this contraction occurs, fine canals radiating from the contractile vacuole are distended with the clear fluid which has probably entered the vacuole from without. Thus a permanent set of water-vessels carry fluid from the contractile vacuole throughout the endosarc.

In such an animal there is a distinct advance of function compared with the amœba: a more elaborate and specialised method of feeding: a more systematic and regular circulation of nutrient matters: a respiratory distribution of water by the contractile vesicle and its water-canals; more rapid motion; and more obvious sensation.

In the bell animalcule, or *Vorticella*, the same kind of division of labour exists, but in one of its commonest conditions it is attached by a thin stalk to the stalk of some weed or other object. Besides the ciliary movement we here find that the general mass of the protoplasm can suddenly and forcibly contract, so as to completely alter its shape, and change the bell into a rounded mass. This spasm of the body is commonly associated with a wonderfully rapid contraction of the stalk. This stalk consists of a delicate transparent sheath, in the centre of which is a thin thread of pale protoplasm. The rapid contraction of the protoplasm of the stalk and the spasm of the bell occur on the application of the least mechanical excitation, such as a touch to the cover-glass. Here in a single cell we have certain portions set apart for special purposes, most of which are the same as in paramœcia. But the animal being attached requires a special way of escaping from its enemies, and hence we find it endowed with three special forms of motion. Besides the ciliary and streaming protoplasmic motion, its body can spasmodically change its shape, and the stalk contracts with a velocity comparable with that of the most specially modified contractile tissue (muscle) of the higher animals, by means of which their rapid and varied movements are carried out.

CHAPTER V.

FOOD.

THE continuation of life depends on certain chemical changes which are accompanied by a loss of substance on the part of the active tissues. This loss must be made good by the *assimilation* of material from without, and the manner in which assimilation takes place constitutes one great point of difference between Plants and Animals. In the majority of the former (certain fungi form the main exceptions) the cells in those portions of the plant which are exposed to the light and air, contain a peculiar green substance called chlorophyll, and through the agency of this substance they are able to obtain from the inorganic kingdom nearly all the food they require. Water, with such salts as may happen to be in solution, is taken up by the roots, and carried through the stem to the leaves ; here the active chlorophyll-bearing cells, under the influence of the sun's rays, cause its elements to unite with the carbon dioxide present in the air, and form various substances, of which we may take starch or cellulose as an example. The reaction may be represented chemically, thus :—

$$6\,CO_2 + 5\,H_2O = \underbrace{C_6H_{10}O_5}_{\text{Starch or cellulose}} + O_{12}.$$

A large proportion of oxygen is thus set free and discharged into the atmosphere.

The most striking property of plant protoplasm is the power of using the energy of the sun's rays to separate the elements of the very stable compounds, carbon dioxide and water, and from the elements thus obtained to make a series of more complex and unstable compounds, which readily unite with more oxygen, and change back to carbonic anhydride and water.

The carbon compounds made in and by the protoplasm of the green plants are some of the so-called "organic compounds," which enter into the composition of both plants and animals, and form an

essential part of the food of the latter. They may be divided into three groups—

i. *Carbohydrates*—bodies so called from the presence of hydrogen and oxygen in proportion to form water ; *e.g.* :—

Starch, $C_6H_{10}O_5 = C_6(H_2O)_5$
Grape-sugar (dextrose) $C_6H_{12}O_6 = C_6(H_2O)_6$
Cane-sugar (sucrose) $C_{12}H_{22}O_{11} = C_{12}(H_2O)_{11}$

ii. *Fats*—compounds of carbon and hydrogen with a less proportion of oxygen than the starches, *e.g.* :
Olein (principal constituent of olive oil), $C_{57}H_{104}O_6$

iii. *Albuminous bodies* which contain nitrogen in addition to carbon, hydrogen, and oxygen. These are of complex composition, and, as a rule, cannot be represented by chemical formulæ.

Animals cannot thrive on the simple forms of food obtainable from the inorganic kingdom, which suffice for the nutrition of a plant. They require for assimilation materials nearly allied in chemical composition to their own tissues ; substances to be used as fuel in producing the activities of their bodies. In short, they require as food the very organic substances which plants spend their lives in making : viz., starches, fats, and albuminous bodies. These substances must be supplied to animals ready made, so that directly or indirectly, through the medium of other animals, all these complex substances are the result of work done by vegetable life.

The chief acts of animal protoplasm are oxidations, a slow burning away of its substance, which results in the production of inorganic materials like those used by plants as food.

Plants use simple food-stuffs, and from them manufacture complex combustible materials, and thus store up the energy of the sun's rays in their textures.

Animals, on the other hand, use complex food-stuffs to renew their tissues, which are constantly being oxidised, and by this means the energy for the performance of their active functions is set free.

Although the various kinds of food-stuffs used by animals are highly organised and like the animal tissues in composition, yet they cannot be admitted at once into the economy without having undergone a special preparation, which takes place in the digestive tract where the various food-stuffs are so changed as to allow them to pass into the fluids of the body.

We shall first consider the food-stuffs, next their preparation for absorption (digestion), and then the means by which they are distributed to the tissues (circulation). The final step in tracing the assimilation of the food is to follow the intimate processes which go on between the blood which carries the nutriment, and the different tissues.

Classification of Food-stuffs.

There are two portals, namely, the lungs and the alimentary canal, by which new materials normally enter the animal body.

Within the lungs the blood comes into close relation with the air, and takes from it oxygen. The oxygen is then carried to the various tissues, where it aids in the combustion accompanying the life and functions of these tissues. Oxygen is the most abundant element in the body, taking part in almost every chemical change, and its continuous supply is more immediately necessary for life than that of any other substance, yet it is not counted as food, because tissue oxidation is distinguished from tissue nutrition.

The details of the union of oxygen with the blood will be found in the Chapter (XIX.) on Respiration.

It is then only to the liquid and solid portions of the material income of an animal—that, in short, which it must busy itself to obtain—that the term "food" is applied. These are introduced into the alimentary canal, where the nutrient materials are separated and prepared for absorption, while the portions which are not useful for nutrition are carried away as excrement. We are, therefore, quite prepared to hear that the really nutritious food-stuffs are composed of materials which are chemically like the tissues, although, as we shall see, we have no grounds for believing that the different chemical groups of nutritive stuffs are exclusively destined to replace corresponding substances in the body. On the contrary, we have good reason to think that within the body the conversion of one group into another is common.

In Chapter III. the tissues of the animal body were shown to consist of chemical compounds, which have been classified into certain groups. It has also been stated that the tissues are constantly undergoing chemical changes inseparable from their life, and that for these changes a supply of nutritive material is necessary.

The nutriment required for an animal is made up of substances which may be divided into the same chemical groups as the tissues of the body : viz, proteids, fats, carbohydrates, salts, and water. So

that each of the various substances which we make use of as food, contains in varying proportions several of the different kinds of nutrient material, either naturally or artificially mixed so as to form a complex mass, the important item water being the only one which is commonly used by itself. These substances may be considered to be the chemical bases of the food, as they are also the chemical bases of the animal body.

The following classification shows the relationships between the chief constituents of food, from a chemical point of view, and their distribution in the various substances we eat.

I. Organic.

1. Nitrogenous—

A. Albuminous—abundant in eggs, milk, meat, peas, wheaten flour, &c.

B. Albuminoid—in soups, jellies, &c.

2. Non-Nitrogenous—

A. Carbohydrates (sugar, starch)—abundant in all kinds of vegetable food, and in milk, and present in small quantity in meat, fish, &c.

B. Fats—in milk, butter, cheese, fat tissues of meat, some vegetables, oils, &c.

II. Inorganic.

1. Salts—mixed with all kinds of food.
2. Water—mixed with the foregoing or alone.

The *nutritive value* of any kind of food depends upon a variety of circumstances, which may be thus summed up :—

I. *Chemical composition*, of which the main points are—

(1.) The proportion of soluble and digestible matters (true food-stuffs) to those which are insoluble and indigestible, such as cellulose, keratin, elastic tissue, &c.

(2.) The number of different kinds of nutrient stuffs present in it.

(3.) The relative proportion of each of these chemical groups.

II. *Mechanical Construction.*—The degree of subdivision in which the substance is introduced into the stomach, materially influences its nutritive value, since the smaller the particles the greater the amount of surface exposed to the action of the digestive juices.

The relation of the nutrient to the non-nutrient parts is also of importance, as is seen where the nutritious starch of various vegetables is enclosed in insoluble cases of cellulose, which, if not burst by boiling, prevent the digestive fluids from reaching the starch.

III. *Digestibility.*—This depends partly upon how the substances affect the motions of the intestines, and partly upon their construction. Thus, some substances, such as cheese, though chemically showing evidence of great nutritive properties, by their impermeability resist the digestive juices, and are not very valuable as food.

IV. *Idiosyncrasy.*—In different animals and in different individuals, and even in the same individuals under different circumstances, food may have a different nutritive value.

Food Requirements.

Chemically foods are composed of a limited number of elements similar to those found in the animal tissues, viz., carbon, oxygen, nitrogen, and hydrogen, together with some salts. If nothing more were needed by the economy than a supply of these elements and salts in a proportion like that in which they exist in the tissues, such could be easily obtained from inorganic sources ; but, as has already been stated, it is necessary that an animal obtain these elements associated in the form of organic materials of complex construction (namely, proteids, &c.). Allowing the necessity of organic food, it might be supposed that since the elements exist in proper proportion in the proteids, an abundant supply of proteids would suffice for all nutritive purposes, and alone form an adequate diet. Theoretically, proteid alone ought to be sufficient for nutrition. It, however, has been frequently tested by experiment, and practically decided, that an animal will not thrive upon a free supply of pure proteid food alone ; and in the human subject such exclusive diet would induce dangerous abnormal conditions in a short time. Since nitrogen is an important element in nearly all parts of the body, we could hardly expect that a diet composed of non-nitrogenous food-stuffs alone could support the animal economy. In short, the results of numerous experiments show that no one group of the food-stuffs enumerated can alone sustain the body, but rather prove that a certain proportion of each is absolutely necessary for life.

Special Forms of Food.

The articles of diet we make use of are *animal* or *vegetable*, according to the source from which they are derived. It will be seen that a varying quantity of all chemical classes of food-stuffs is present in most kinds of food, whether animal or vegetable. The following diagram shows the proportion of the more important food-stuffs in some examples of the materials commonly used as food :—

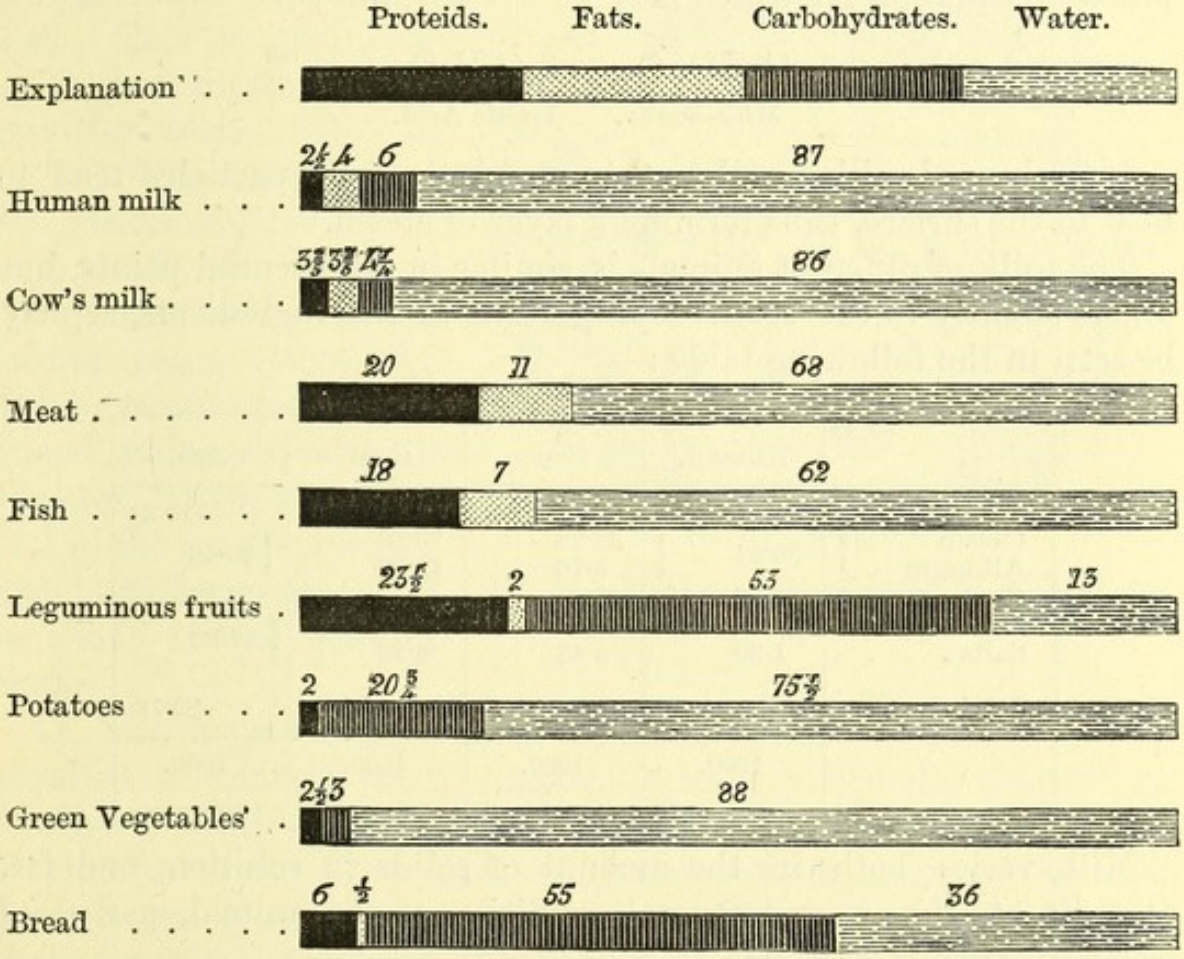


Fig. 42.—Diagram showing the proportion of the principal food-stuffs in a few typical comestibles. The numbers indicate per-centages. Salts and indigestible materials omitted.

Among animal foods are included milk, the flesh of various animals, and the eggs of birds. These may be more fully described as typical examples.

Milk.—For a certain period of their lifetime the secretion of the mammary gland forms the only food of all mammals, and it is the one natural product which when taken alone affords adequate nutriment.

It consists of a slightly alkaline watery fluid, containing :—

1. Proteids, casein and albumin in solution.
2. Fats, finely divided to form perfect emulsion.
3. Carbohydrate, sugar in solution.
4. Salts, in solution.
5. Water.

Owing to the action of certain organisms which readily propagate in milk, if exposed to the air at a warm temperature for some time, it loses its alkaline reaction, and becomes sour from the formation of lactic acid from the milk-sugar, by a kind of fermentation, the probable equation for which may be written thus :—

$$\underset{\text{Milk-Sugar.}}{C_6H_{12}O_6} = 2\,\underset{\text{Lactic Acid.}}{C_3H_6O_3}.$$

If fresh good milk be allowed to stand, the fatty particles tend to float to the surface, thus forming a layer of cream.

The milk of different animals is similar in all essential points, but differs slightly in the relative proportion of the ingredients, as may be seen in the following table :—

	Human.	Cow.	Goat.	Ass.
Water . . .	889·08	857·05	863·58	910·24
Casein . .	39·24	48·28	33·60	20·18
Albumin .		5·76	12·99	
Butter . . .	26·66	43·05	43·57	12·56
Milk Sugar .	43·64	40·37	40·04	57·02
Salts	1·38	5·48	6·22	
Solids . . .	110·92	142·95	136·42	89·76
	1000.	1000.	1000.	1000.

Milk varies both in the amount of solids in solution, and fat, according to the age and general condition of the animal, period of lactation, time of day, &c.

Since human milk is much poorer in proteid, fat, and salts (see Table), and richer in sugar, than that of the cow and other domestic animals, it is necessary to dilute the latter with water, and add sugar, when it is substituted for human milk in feeding infants.

The great value of milk as nutriment depends upon the fact that it contains every class of food-stuff, viz., proteids, fat, carbohydrates, salts, and water, in the proportion demanded by the economy; the salts in milk being those required for building up the bones of the infant, viz., phosphates and carbonates of lime, &c.

The normal variations in these proportions are not very great, but

as adulteration with water is common, a knowledge of the method of testing the purity of milk is necessary.

Milk Tests.—The specific gravity of milk gives an easy measure of the solids in solution, but unfortunately it gives no accurate estimate of the amount of fat suspended in the emulsion. Therefore, to test milk adequately two methods must be employed: one to estimate the degree of density of solution, and the other the degree of opacity of the emulsion.

I. To test the density, a specially graduated form of hydrometer is generally used. This is graduated so as to indicate specific gravities from 1014 to 1042. The latter being the maximum density of pure milk, (the average being about 1030), and the former being about the density of pure milk when mixed with an equal bulk of water. Every reduction of 3 in the specific gravity may be said to correspond to about 10 per cent of water.

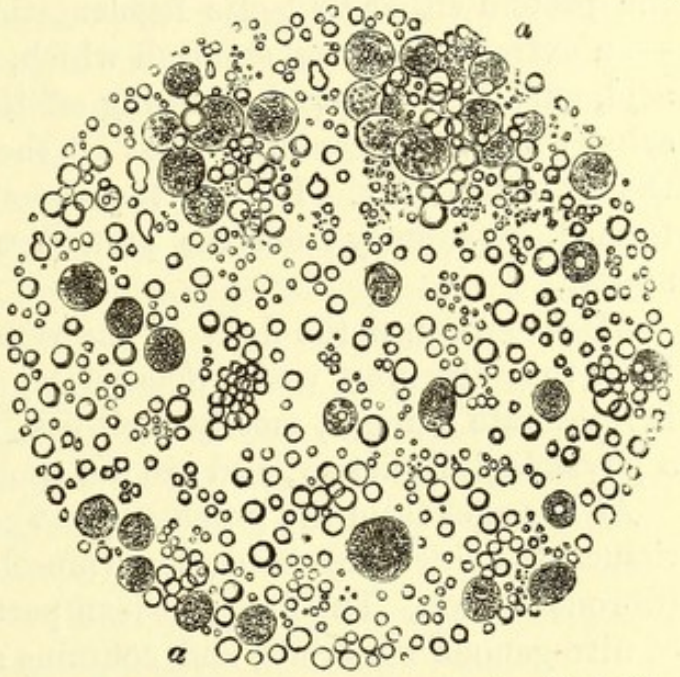


Fig. 43.—Microscopic appearance of milk in the early stage of lactation, showing colostrum cells (*a*).

II. The degree of opacity is estimated by the amount of water required to render a small quantity of milk sufficiently translucent to allow a candle-flame to be seen through a layer of the mixture one centimetre thick. One cubic centimetre of the milk (which has been shown by the microscope and the iodine test not to contain chalk or starch) is placed in a test-glass with flat parallel sides, just one centimetre apart, and water is cautiously added from a graduated pipette. The more water required the richer the milk is in fat; good fresh milk requires about 70 times its bulk of water to become translucent.

Another method employed for the same purpose consists in the comparison of the colour produced by a layer of milk 1 mm. thick in a black cell with a previously prepared standard of greyish colours.

The quantity of fat may also be estimated by placing the milk in a tall graduated vessel for twenty-four hours, at the end of which time it should show at least 10 per cent. of cream.

Butter is made from milk, or better from cream, by breaking by agitation the coating of proteid which before churning prevents the oil globules from running together. It is almost completely composed of fat, the larger globules having run together to form the solid butter, which can be removed, leaving some small fat globules with the proteids, milk-sugar, lactic acid, and salts in the water forming "butter-milk."*

Cheese is another form of food made from milk by precipitating the proteid either by lactic fermentation, or the addition of rennet —an extract of calves' stomach which, without the presence of any acid, curdles milk—and draining off the solution of milk-sugar, and salts (whey). It contains most of the proteid, and a great deal of the fat of the milk. During the ripening of the cheese more fat is formed, apparently from the proteid, while leucin and tyrosin also appear.

Meat.—We use the flesh of the vegetable-feeding mammals and birds that are most easily obtainable, and many kinds of fish. The invertebrate animals, mostly shell-fish, need hardly be mentioned in a physiological dietary, and are not spoken of as meat.

As it comes from the butcher, meat consists of many of the animal tissues, the chief ones being flesh (muscle tissue), fat, and some sinews (fibrous tissue). The fleshy or lean part of meat is chiefly made up of nitrogenous materials, and contains : (1) Several proteids, chiefly the globulin, *myosin ;* (2) gelatine yielding substances ; (3) carbohydrates, as inosit and grape-sugar ; (4) small quantities of fat ; (5) several inorganic salts ; (6) extractives.

Meat may be eaten raw, but as it is impossible to impart to it the various flavours which our artificial tastes demand without some special preparation, it is generally cooked before use. Moreover, the not infrequent occurrence in muscle of parasites which would prove injurious if swallowed alive, makes the exposure of meat to a temperature high enough to ensure their destruction advisable.

Apart from pleasing the taste, it is of great importance so to prepare meat as to preserve in it all the nutrient parts, many of which are soluble in water, and therefore are apt to be removed if that solvent be injudiciously used. Thus, the process of roasting, in which all its nutrient parts are retained, ought to be more satisfactory than boiling, by which the salts, extractives, carbohydrates, gelatin, and some albumin may be dissolved by the water. However, if the meat be plunged into water which is already boiling, the proteids near the

* For the details of secretion of milk, &c., see Mammary Gland.

surface are rapidly coagulated, and the water cannot reach the central parts in sufficient quantity to remove even the soluble ingredients. The whole of the albuminous parts may be thus coagulated as the temperature of the inner parts rises to boiling point. In treating meat to obtain "stock" (bouillon) for the foundation of soups, the opposite procedure is adopted. Cold water is used, and the temperature slowly and gradually raised, but not quite to boiling point, in order that as much as possible of the soluble materials may be extracted, and a tasteless friable muscle tissue remains ("bouilli"). As the fluid is generally allowed to boil in order to clear it, much of the proteid material which was dissolved in the earlier stage is coagulated and removed with the scum. Although "stock" cannot contain any great proportion of the most important constituents of meat, it is of much value as a nutriment in medical practice, possibly on account of some stimulating action of its ingredients upon the motions of the intestines and heart. A strongly albuminous extract of meat, "beef-tea," may be made by digesting flesh in a small quantity of water, keeping the temperature below that at which albumin coagulates, and adding vinegar and salt to facilitate the formation of syntonin and the solution of myosin. The salt can be then removed by dialysis.

Eggs.—Eggs consist of two edible parts, one, the white, composed of albumin, and the other, the yolk, chiefly made up of fat.

The white is concentrated watery solution of albumin, held together by delicate membranous meshworks. Besides the albumin it contains traces of fat, sugar, extractives, and salts.

The yellow fat emulsion of the yolk contains a peculiar proteid, vitellin, some grape-sugar, and some inorganic salts, in which combinations of phosphoric acid and potassium are conspicuous. Raw eggs are easy of digestion, as is all albumin in solution. Hard boiled eggs, if not finely divided by mastication, are very difficult to digest, for the gastric juice cannot penetrate the hard masses of coagulated albumin which are so easily and commonly swallowed. Eggs, when lightly cooked, are easily digested, as the albumin is only partially coagulated, and cannot be introduced in large masses into the stomach. Eggs are of very great nutritive value, as they contain so large a per-centage of proteid, fat, and salts.

Vegetable Food.—Vegetables differ from animal food :—

(1.) In containing a much greater proportion of material which for man is indigestible (cellulose), and a less proportion of nutritive material.

(2.) The per-centage of proteid is below that of animal food, and

the proportion of carbohydrates is generally much greater, while the amount of fat is small, but varies considerably. In order, therefore, to get the required amount of nutritive material from a purely vegetable diet, it is necessary to consume a much greater quantity, and the amount of excrement indicating the indigestible matters is proportionately increased.

Cereals.—The most valuable forms of vegetable foods are those obtained from the seeds of certain kindred plants (*Graminaceæ*)—wheat, rye, maize, oats, rice, &c.; which when ground are used either as "whole meal," or, the integument ("bran") being removed, as flour. They contain different kinds of proteid. (1.) A native albumin soluble in water and coagulable by heat, and in many respects like animal albumin; but as it cannot be obtained pure it is imperfectly known. (2.) Vegetable fibrin, an elastic body, which coagulates spontaneously and is difficult to separate. (3.) Vegetable glue or gliadin, which gives the peculiar adhesiveness to the *gluten*, as the proteid mixture obtainable from corn is commonly called. Cereals also contain traces of fat, and a very large proportion of starch and some salts.

The following table gives the per-centages of the chief different nutritive stuffs in some common cereals :—

	Wheat.	Barley.	Oats.	Maize.	Rice.
Water	13	14·48	10·88	12	9·20
Proteid	13·53	12·26	9·04	7·91	5·06
Fats	1·58	2·63	4·	4·83	·75
Carbohydrates . .	69·61	67·96	73·49	73·19	84·47
Salts	2·	2·65	2·59	1·28	·5

Green Vegetables.—These contain some starch, sugar, dextrin, salts, and minute quantities of proteid, and are of small nutritive value.

Potatoes contain very little proteid, but a considerable quantity of starch, upon which their nutritive value almost entirely depends.

The following table gives the relative proportions of the various *nutritive materials* contained in some of the common vegetable foods :—

	Peas.	Beans.	Potatoes.	Cauliflower.
Water	14·50	12·85	72·74	79·18
Proteid	22·35	22·	1·32	·50
Carbohydrates . .	56·61	56·65	23·77	18·
Extractive . . .	1·18	3·32	·97	
Fats	1·96	1·59	·15	
Salts	2·37	2·53	1·05	·7

The most striking points are the very large proportion of proteid in the leguminous fruits, and the comparative richness of all vegetables in starchy food-stuffs.

Water is the great medium by which food is dissolved, and made capable of ingestion. Spring-water always has a certain quantity of lime and other salts in solution, and in proportion to the amount of salts is said to be "soft" or "hard." Water is tasteless, inodorous, and colourless when pure. Soft water, such as rain-water, is pure, but not so agreeable to taste as spring-water, and is very liable to contamination in passing through gutters, &c., previous to collection. Standing water should be avoided for drinking, owing to the probability of its containing organic matter.

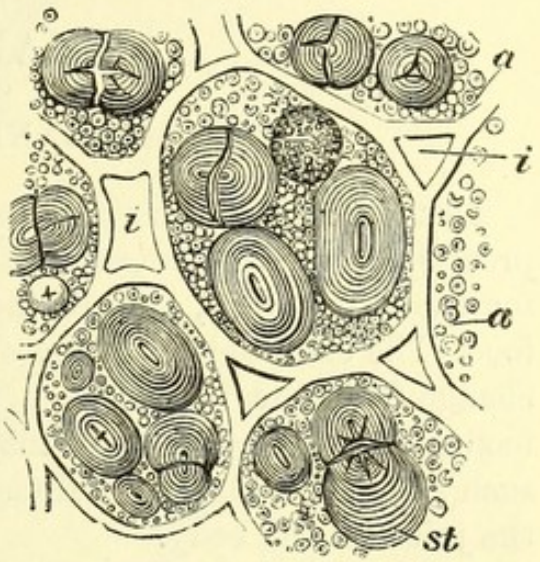


Fig. 44.—Section of Pea, showing starch and aleurone granules imbedded in the protoplasm of the cells. (After Sachs.)
a.—Aleurone granules.
st.—Starch granules.
i.—Intercellular spaces.

Since water is known to be a common means of communicating disease, care must be taken as to the source of drinking water, and we should be able to form an opinion as to its purity when its source is not known. It is, perhaps, impossible to detect in it the specific impurity which causes any disease, but there are some characters supposed to be commonly associated with its pathogenic properties which can be easily recognised, and should be familiar to a student of Physiology. The want of brilliant limpidity must be regarded with suspicion. Any kind of smell, disagreeable or not, indicates impurity. The reduction (loss of colour) of permanganate of potash, when added in small quantity to acidified water, indicates the probable presence of organic matter. A high per-centage of chlorides is often associated with sewage contamination.

Salts.—Great varieties of salts are taken into the system, of which chloride of sodium forms the largest proportion. These have no doubt very important functions to perform, in entering into combination with the various tissues, and also probably in aiding the chemical changes of parts of which they do not form a normal constituent. They help to render certain substances soluble, and stimulate the cells of certain glands to more active secretion, *e.g.*, the kidney excretes more urea when there is an abundant supply of common salt in the food.

CHAPTER VI.

THE MECHANISM OF DIGESTION.

THE acts of digestion may be divided into *mechanical* and *chemical* processes. Under the *mechanical* processes come the arrangements for the subdivision, onward movement, and general mixture of the food. The chief objects of the *chemical* changes may be said to be the change from the insoluble to the soluble form of certain kinds of food-stuffs (starch and proteids) and the finer subdivision of others, such as fats, which do not dissolve in the intestinal secretions or in the juices of the body.

Attention has already been called to the fact that there are different kinds of contracting textures, and that they are capable of different kinds of motion, some slow and steady, some rhythmical, some sharp, short and sudden. It must also be remembered that the more energetic and sudden the motions are, the more marked becomes the differentiation of the tissue. Thus the active, quick-contracting skeletal muscles and the rhythmically acting heart, are made up of tissue which is very distinct in structure and in mode of action from that of the contracting cells composed of ordinary protoplasm, while in the slowly moving internal organs we meet tissue elements which in different animals show many stages of gradation between simple, indifferentiated protoplasm and the special striated muscle tissue.

It is necessary that in the first stages of alimentation the motions should be quick and energetic ; so the mouth, pharynx, and upper part of the œsophagus are supplied with striated muscle tissue, which differs in function and structure from that of the rest of the alimentary canal. In the stomach and intestines slower and more gradual kinds of motion are required, and here we find a good example of non-striated muscle tissue.

Around the extremity of the rectum is a band of smooth muscle, which remains in a condition of continuous or *tonic* contraction.

For further details concerning the muscle tissue the student must

turn to the Chapter (p. 366) on that subject. Here, however, it may not be out of place to describe briefly the special character of

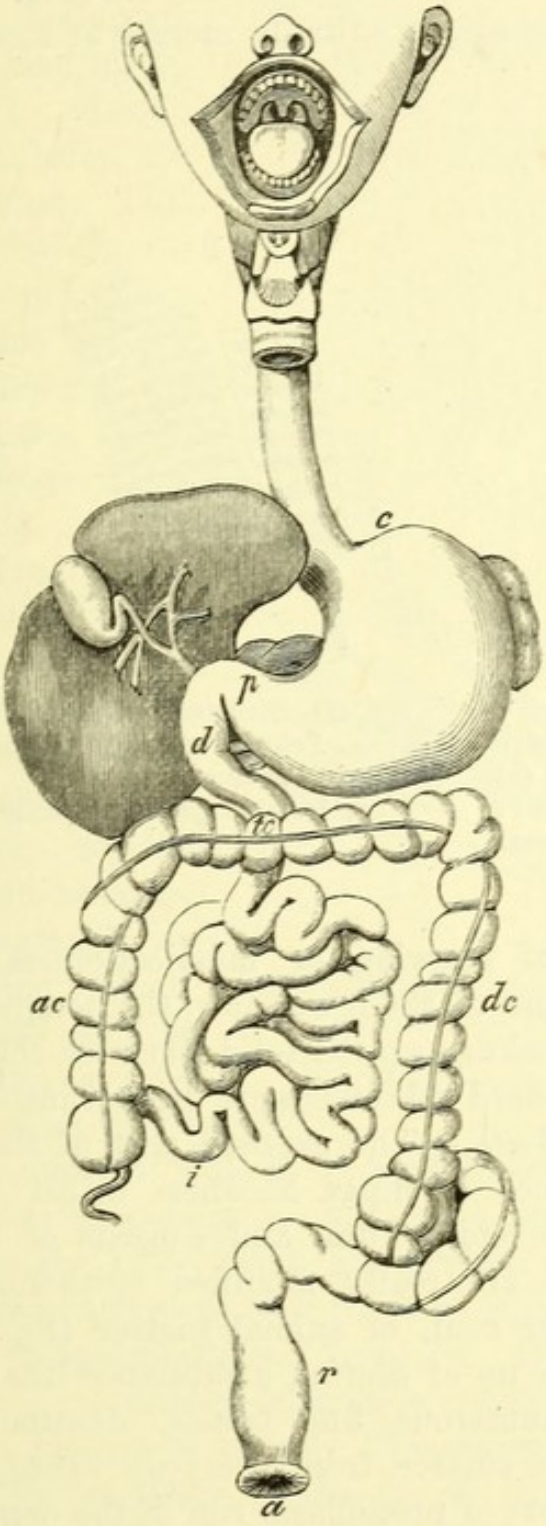


Fig. 45.—Diagram of Alimentary Tract, &c. Angles of mouth slit to show the back of the buccal cavity and the top of the pharynx. *(c)* Cardiac; *(p)* Pyloric parts of stomach; *(d)* Duodenum; *(i)* Jejunum and Ilium; *(ac)* Ascending, *(tc)* transverse, and *(dc)* descending colon; *(r)* Rectum; *(a)* Anus.

the muscles found in the wall of the digestive tube and their general arrangement.

Mastication.—In man, the introduction of food into the mouth is generally accomplished by artificial means, so that the biting teeth (incisors) and the tearing teeth (canines) are (Fig. 46) comparatively little used for obtaining a suitable morsel of food. In the mouth

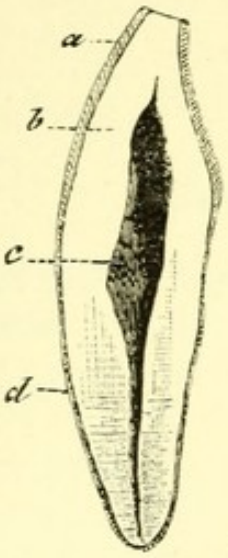


Fig. 46.—Vertical section of the Canine Tooth of a man. (*a*) Enamel; (*b*) Dentine; (*c*) Pulp cavity; (*d*) Crusta petrosa. (Cadiat.)

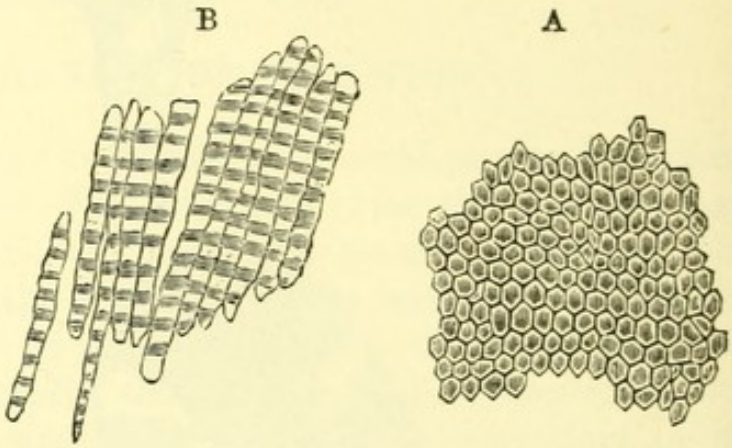


Fig. 47.—Structural elements of the Enamel of Tooth
A. Prisms cut across showing the hexagonal section.
B. Isolated prisms. (Kölliker.)

the essential act of chewing or mastication is accomplished by means of the motions of the lower jaw, the tongue, and the cheeks. This process of breaking up the solid parts of the food ought to be continued until all hard substances are ground into a soft pulp.

Structure of the Teeth.—The exposed part of the teeth is covered by a dense substance of flinty hardness called *enamel*, which is developed from the epithelium, and consists of hexagonal prisms set on end, which are really modified epithelial cells but only contain about 2 per cent. of animal matter (Fig. 47). The bulk of the tooth is made up of *dentine*, a substance like bone in composition, pierced by numerous fine canals, dentine tubules, which radiate towards the surface, from the *pulp cavity*, in the centre of the tooth. Filaments of protoplasm run in the dentine tubules from the tooth cells, which line the pulp cavity and preside over the nutrition of the tooth. The cavity contains vessels, nerves, &c., which enter at the root of the tooth which is enclosed in a kind of modified bone tissue called *crusta petrosa*.

The two rows of grinding teeth, composed of molars and premolars, of the lower jaw are made to rub against the corresponding teeth

in the fixed upper jaw by the combined vertical and horizontal movements induced by the action of the powerful muscles of mastication, the temporal muscles, together with the masseters and internal pterygoids, all tending by their contraction to elevate the lower jaw and bring the teeth forcibly together. This action is opposed by the digastric, the genio- and mylohyoid muscles, which by their combined force depress the jaw and separate the teeth. The horizontal movements are in the main accomplished by the external pterygoid muscles, which, acting together, pull the lower jaw forward so as to make the lower teeth protrude beyond the upper. In this action they are opposed by the digastric and hyoid muscles. One external pterygoid on either side acting alone, advances that side of the lower jaw only, and thereby causes the lower teeth to incline towards the opposite side in a lateral direction. The two muscles acting alternately cause a horizontal motion from side to side. Thus, while the lower teeth are pressed firmly against the upper ones they are at the same time made to glide over them, either from side to side or backwards and forwards. By these movements the bruised food is soon pushed from between the teeth, and passes towards either the tongue or cheek. The morsel is soon replaced between the teeth by the action of the tongue on the one hand and the buccinator muscle in the cheek on the other.

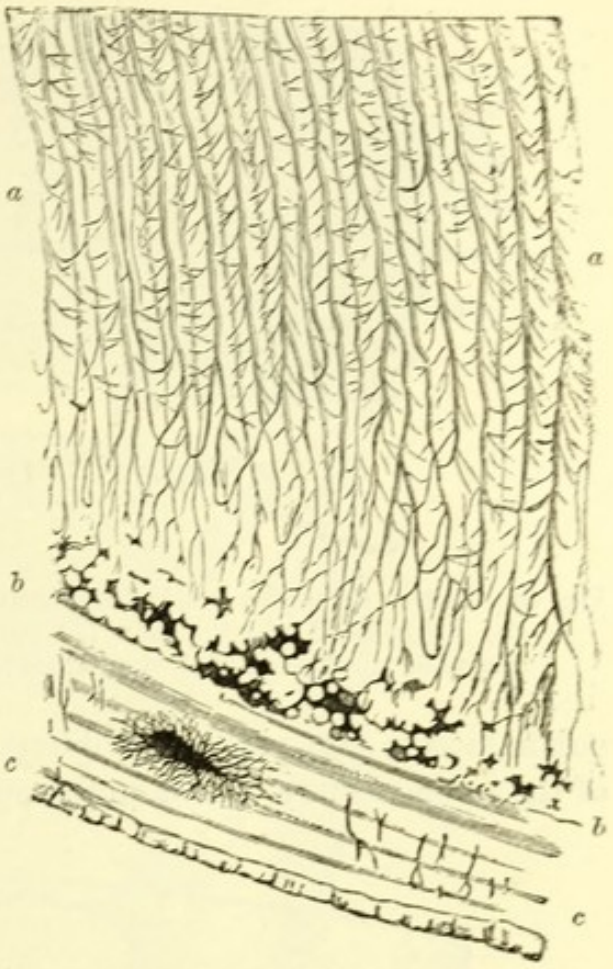


Fig. 48.—Section through a portion of the fang of a tooth. (*a*) Dentine tubules near the surface of the fang; (*b*) Granular layer; (*c*) Crusta petrosa.

While the process of mastication is going on, the food becomes thoroughly moistened with the fluid secreted within the mouth.

DEGLUTITION.—The next step is swallowing. When the food is sufficiently triturated and moistened it is collected together by means

of the tongue, and placed upon the upper surface of that organ, which becomes concave and presses or rolls the soft pulp against the hard

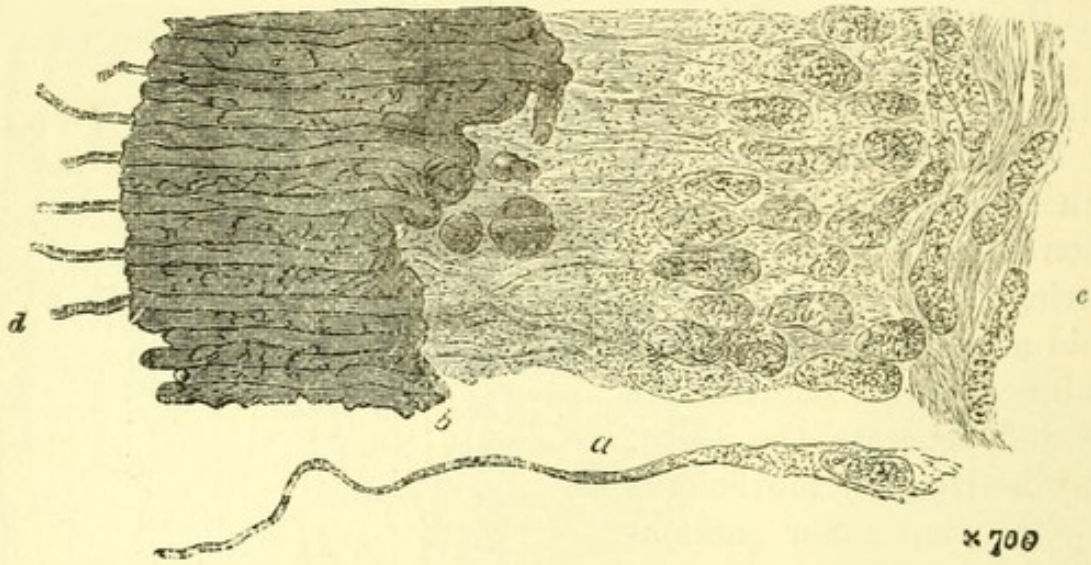


Fig. 49.—Section through a portion of dentine next the pulp cavity of a growing tooth. *(a)* An isolated odontoblast; *(b)* Growing part; *(c)* Odontoblasts; *(d)* Filaments of protoplasm projecting from the tubules of hard dentine. (Beale.)

palate so as to shape it into an oblong mass or bolus (Fig. 51). The apex of the tongue is now raised and pressed against the hard palate, and by

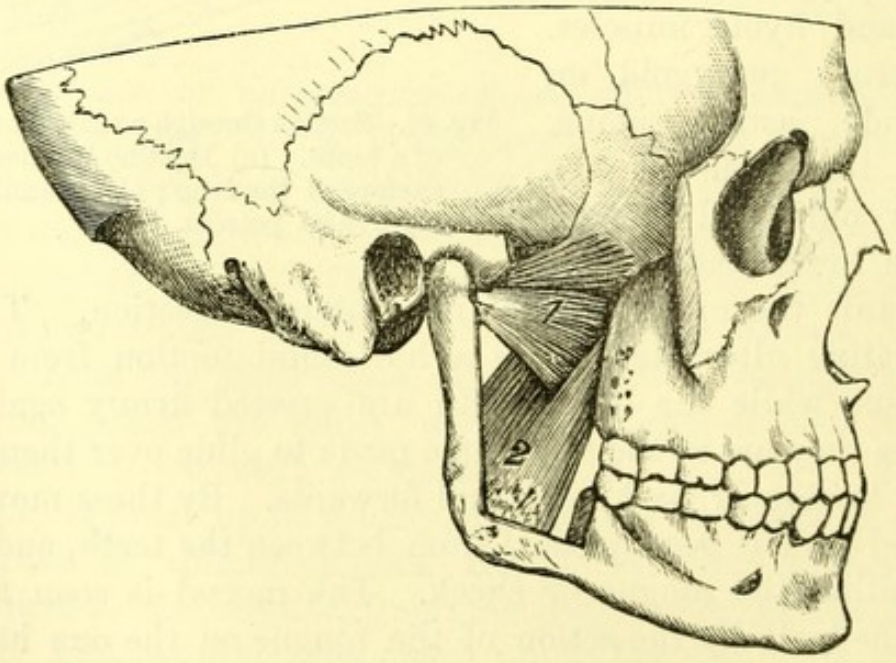


Fig. 50.—The Pterygoid Muscles seen from without after removal of the superficial parts, the temporal muscle, the zygomatic arch, and a portion of the lower jaw and masseter. (1) External, (2) Internal pterygoid muscle.

the successive elevations of the different parts of the dorsum of the tongue the bolus is gradually pushed backwards towards the isthmus of

the fauces. The root of the tongue with the hyoid bone is at the same time drawn upwards and forwards, so that the bolus easily slips down along the retreating slope leading from the mouth cavity, and gets within the reach of the constrictors of the fauces. Immediately before the morsel of food is grasped by the muscles of the fauces the levator palati draws the soft palate upwards and backwards to completely close the posterior openings of the nasal cavity, as is shown by the fact that during the act of swallowing the pressure in the nasal cavity is raised. At the same moment the intrinsic muscles of the larynx, which surround the rima glottidis like a constrictor, firmly close that opening by approximating the cords and arytenoid cartilages. The entire larynx is at the same time drawn up behind the hyoid bone by the thyro-hyoid muscle. The rima glottidis is thus tucked in under the cushion of epiglottis, while the leaf of the epiglottis is pulled down over the larynx by the oblique aryteno-epiglottidean and thyro-epiglottidean muscles.

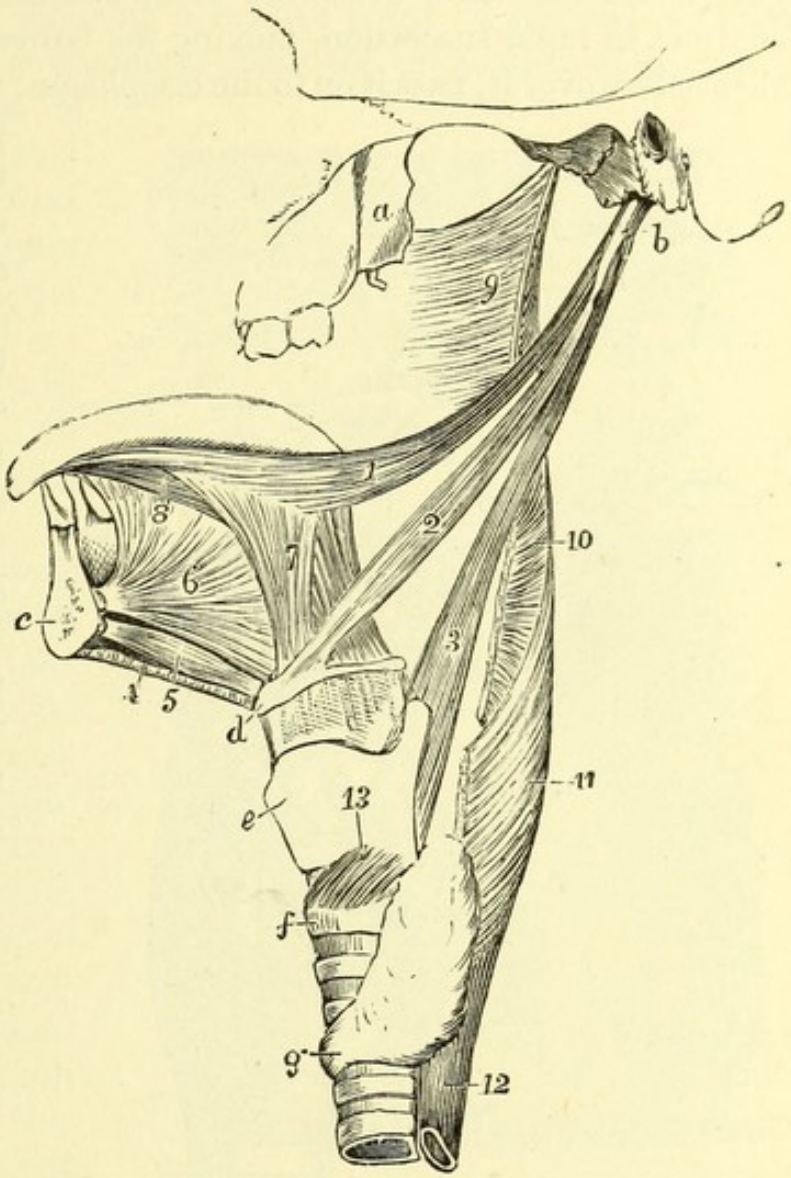


Fig. 51.—Muscles of Tongue and Pharynx.

1, 2, 3, Muscles from styloid process (*b*) to the tongue, hyoid bone (*d*) and pharynx respectively; 4, 5, 6, 7, 8, muscles of tongue; 9, 10, 11, constrictors of pharynx; 12, œsophagus; 13, is placed on larynx (*e*). (Allen Thomson.)

While the closure of the nasal and pulmonary air passages is going on, the bolus has passed out of the cavity of the mouth and has been caught by the palato-glossal and palato-pharyngeal muscles which force

it into the pharynx, and at the same time close the isthmus faucium behind the descending morsel. The stylo-pharyngeis and the pharyngeal constrictors now grasp the bolus spasmodically, and the latter contract in rapid succession, moving the bolus onwards, and drawing themselves over it, pass it on to the œsophagus, where, by a progressing ring-like contraction of the circular muscles and a simultaneous shortening of the longitudinal layer of fibres the mass is slowly squeezed down to the cardiac orifice of the stomach. The movements of the œsophagus are essentially peristaltic in character, the peculiarities of which form of motion will be discussed when speaking of the intestinal movements.

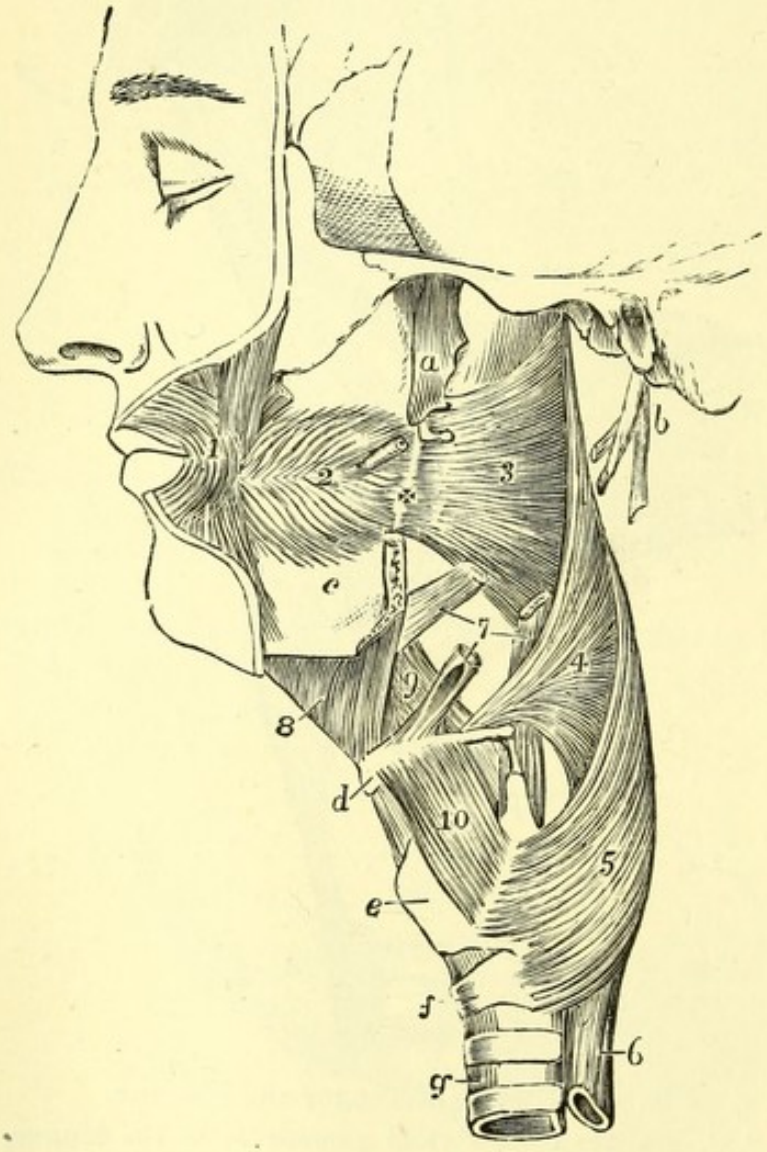


Fig. 52.—Deep Muscles of Cheek, Pharynx, &c.

(1) Orbicularis oris; (2) buccinator; (3) superior, (4) middle, and (5) inferior constrictors of the pharynx; (6) œsophagus; (7) styloid muscles cut across; (8, 9, 10) muscles attached to the hyoid bone (*d*) and thyroid cartilage (*e*). (Allen Thomson.)

The process of swallowing is performed by a continuous series of co-ordinated muscular movements, quite independent of gravitation, as may be seen in animals drinking with their heads downwards. Although these complex sets of movements follow each other regularly and without any check or interval, the act of deglutition is commonly divided into three stages, between which, as there is no pause, it is not easy to draw a hard and fast line.

The *first stage* is simply the initiatory step of placing the morsel of food or some liquid in such a position as to excite the second or spasmodic act of deglutition. This first step is a voluntary act, and it is the only part of the movements of swallowing over which we

can exert complete control. The progress of the morsel between the tongue and palate towards the fauces may be as slow and gradual as we wish, but the moment a certain point is reached volition is at an end, and we are unable to check the completion of the act.

By the *second stage* is meant the period occupied by the passage of the food bolus through the pharynx and past the top of the larynx. Although we are not able to influence it in any way by our will, we are conscious of the food passing in this region. It is a rapid involuntary spasm in which a great number of muscles take part, all of which are made up of striated muscle tissue.

The *third stage* includes all the rest of the time during which the bolus is passing from the grasp of the lower pharyngeal constrictor and along the œsophagus. Not only has our will no influence over this stage of deglutition, but we are hardly conscious of its taking place, since no sensations accompany the greater part of it. Thus the more essential movements of the act of swallowing are purely reflex and involuntary, though we can call forth this series of reflexions by voluntary stimulation of a certain part of the fauces by means of a morsel of food or a drop of liquid. And without such a stimulus as food or liquid we cannot by our will excite swallowing. We think we can perform the muscular movements of swallowing when we please, without any food or fluid, but in this we are mistaken, as careful observation of our own performance of the act will show.

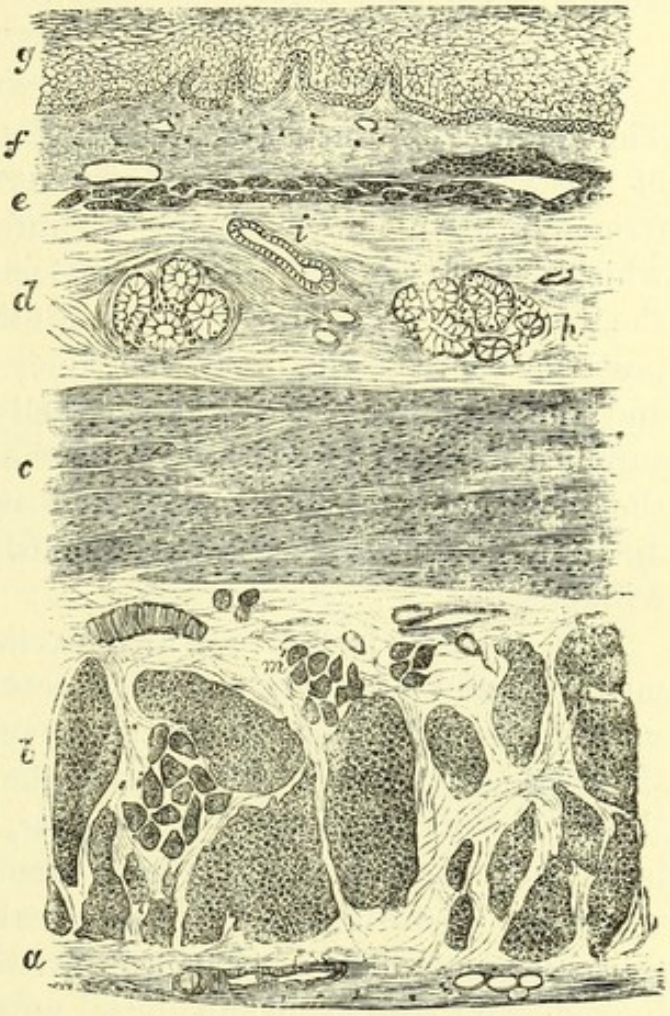


Fig. 53.—Transverse section of Œsophagus. (Horsley.)

a. Outer fibrous covering.
b. Bundles of longitudinal muscle cut across.
c. Transverse muscular coat cut obliquely.
d. Sub-mucous coat with glands in section.
e. Muscular layer of the mucous membrane.
f. Mucous membrane with cut vessels.
g. Stratified epithelium.

The pharyngeal spasm is always preceded by the deposition in the region of the isthmus faucium of some drop of saliva collected from the mouth or fauces themselves. In fact, without a slight preliminary movement of the posterior part of the tongue—which might be called the last act of mastication—the more essential stages of deglutition cannot be excited.

Nervous Mechanism of Mastication and Deglutition.—The voluntary influences which regulate the motions of the muscles of mastication pass along the efferent branches of the fifth nerves (trigemini) which accompany its inferior division. The muscles which depress the jaw to open the teeth and the intrinsic muscles of the tongue are supplied by the ninth pair of nerves (except the posterior belly of the digastric, which has a branch from the facial, and the mylohyoid and anterior belly of the digastric, which are supplied from the third division of the fifth). The co-ordination of the movements of mastication and suction seem to reside in the medulla oblongata, but are obviously under the control of the will.

The afferent impulses which excite the nerve centres in the medulla, and give rise to reflex acts which cause the swallowing movements, pass from the mucous membrane of the fauces along (1) the descending palatine branches of the spheno-palatine ganglion and the second division of the trigeminus, also along (2) the pharyngeal branches of the superior laryngeal branch of the vagus to the medulla, where the co-ordination of pharyngeal spasm and œsophageal peristalsis is accomplished. Thence the efferent impulses pass by (1) the hypoglossal to the hyoid and glossal muscles, (2) the glosso-pharyngeal and vagus to the pharyngeal plexus to supply the constrictors, and (3) the facial and fifth to supply the fauces and palate, as indicated by their anatomical distribution.

The act of deglutition can be readily excited in an animal which is deprived of all the nerve centres down to the medulla oblongata, and may also be seen in those human monstrosities (anencephalous fœtus) without the upper part of the brain being developed, but which can notwithstanding both suck and swallow.

The movements of the œsophagus are reflections from the central nervous system (medulla), both sets of impulses (possibly the afferent and certainly the efferent) passing along the branches of the vagus.

It would appear that the normal peristaltic movements of the œsophagus are always initiated by a pharyngeal spasm, and that they

form an inseparable sequel to it. Thus the wave of contraction passes along the entire length of the œsophagus, even when the bolus is stopped mechanically, and on the other hand a body introduced into the œsophagus without passing through the pharynx excites no peristaltic wave and remains motionless.

But it has been observed, in apparent contradiction to the foregoing statement, that the œsophagus when removed from the body, and therefore quite independent of the pharynx and its nervous connections, can be excited to move peristaltically. In this case the medulla or vagus can have no part in bringing about this wave of movement. To explain this discrepancy it may be urged that the local nerve and muscle mechanism in the tissues of the œsophagus are capable by themselves of carrying out peristaltic contraction independently of the central nerve organs, but that this power is, under ordinary circumstances, held in check by the vagus. The inhibition is temporarily suspended as a sequence of pharyngeal spasm, and consequently a wave of peristaltic contraction is excited in the œsophageal muscles, either in response to the direct stimulus of a passing bolus, or as a result of impulses reflected along the vagus channels from the medulla.

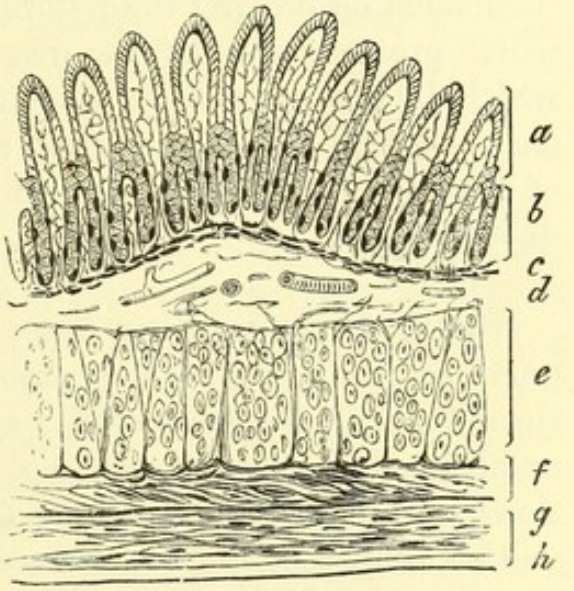


Fig. 54.—Diagram of Wall of the Stomach showing the relative thickness of the mucous membrane (*a*, *b*, *c*), and the transverse (*e*), oblique (*f*), and longitudinal muscle fibres.

Motion of the Stomach.—The stomach and greater part of the intestinal tract move freely within the abdomen, being covered by the smooth serous lining of that cavity, which also keeps in position, so as to restrict their movements, those parts, such as the duodenum, into which the ducts of large glands open. When the stomach is empty it hangs with the great curvature downwards, and the muscular coats are quiescent. On being filled it is passively rotated on its long axis, so that the greater curvature is turned forwards, here meeting with less resistance, and the lesser curvature is turned backwards to its line of attachment. In the main, the motions of the stomach are peristaltic. They become very active about fifteen minutes after the introduction of food, and gradually become more

and more energetic until the end of stomach digestion, which lasts about five hours.

The result of the peristaltic motion is to move the food, particularly the part next the gastric wall, along the great curvature towards the pylorus. A back current towards the cardiac extremity has been noticed running along the lesser curvature, and the median axis of the food mass. At the same time a peculiar rotatory motion of the gastric wall takes place, similar to that of rolling a ball between the palms of the hands, so that the food is twisted in a given direction, and the deeper lying portion is brought into contact with the mucous membrane.

While the fundus keeps up considerable pressure on the contents of the stomach, the indistinct peristaltic action of the central parts is intensified on nearing the pylorus into a strong circular contraction, which proceeds as a definite wave towards the pyloric valve, through which it gradually forces the more or less digested food. At first only the fluid parts are allowed to pass, but towards the later stages of digestion the fatigued pyloric muscle admits solid masses into the duodenum.

Nerve Influence on Stomach Motions.—The stomach has nerve connections with the cerebro-spinal axis through the vagi, and the splanchnic branches of the sympathetic, and in the walls of the organ itself are numerous ganglion cells. The sympathetic connections do not seem to have any influence on the muscular coats, for neither their stimulation nor section has any marked effect on their movements. If the vagi be severed, stomach contractions still occur, but no form of local stimulation produces the normal gastric motions, even if the organ be quite full of food, therefore it would appear that the local nerve centres are not sufficient to excite the normal rhythmical muscular action. Moreover, stimulation of the cut vagi leading to the stomach causes active movements when the stomach is full. It is not merely the presence of food that produces the movements, as is shown by the fact that the motions increase as the contents of the stomach diminish, but conditions incidental to digestion (hyperæmia, &c.) probably also act as a stimulus.

Vomiting is the ejection of the contents of the stomach by means of a convulsive action of the respiratory and abdominal muscles associated with an abnormal contraction of the stomach wall, which aids in opening the cardiac orifice while it keeps the pylorus firmly closed.

The act of vomiting is commonly preceded by (1) a feeling of sickness or nausea, (2) a great secretion of saliva, (3) retching. The latter consists in a violent inspiratory effort in the midst of which the root of the tongue and the larynx are raised and the rima glottidis suddenly closed so as to prevent air entering the wind-pipe. The inspiratory muscles still acting, and the pharynx and upper part of the œsophagus being held open, air is drawn into the gullet and dilates this tube nearly as far as the opening into the stomach. A contraction of the muscle fibres radiating from the œsophagus over the stomach, then opens the cardiac orifice and allows some gas to escape. Now the act of vomiting is completed if at this moment—the mouth and pharynx being open, the larynx closed, the œsophagus on the stretch, the cardiac orifice relaxed, and the pylorus firmly closed—the expiratory muscles forcibly contract, and, pressing upon the abdominal cavity, give a sudden stroke to its contents so as to empty the stomach. The wall of the stomach also contracts evenly throughout, but not with any forcible anti-peristaltic action such as would greatly aid in the operation of rapidly ejecting the vomit. The chief object attained in the adult by the action of the muscular coat of the stomach seems to be the relaxation of the cardiac orifice. In children, when the fundus is little developed, and the fibres radiating over the stomach from the œsophagus are numerous and strong, the act of vomiting requires less effort on the part of the respiratory muscles, the frequent puking of suckling infants being accomplished by the gastric muscle alone. When the vomit is emitted, the hyoidean, laryngeal, and neck muscles relax, and the air is forcibly driven out of the partially distended lungs so as to clear away any remaining particles from the upper part of the air passages.

Vomiting is usually caused by irritation of the stomach itself, and may be induced by either mechanical, electrical, or chemical stimulation of the mucous membrane. In this way some emetics, such as mustard, sulphate of copper, &c., act. It may also be caused by intestinal irritation, as when a hernia is strangulated, or the mucous membrane irritated by intestinal worms.

Gentle stimulation of the fauces and neighbourhood of the root of the tongue commonly induces vomiting. In the early stages of pregnancy the unusual condition of the uterus causes frequent vomiting, which is known as "morning sickness." The irritation of a calculus passing through the ureter, or a gall-stone impacted in the bile duct, usually excite vomiting. Injuries of the brain, and psychical impressions, particularly those excited by the sense of

smell or unusual disturbance of equilibrium, may give rise to vomiting. Moreover, a number of medicaments, as apomorphin, emetin, &c., cause vomiting if introduced into the blood.

From the foregoing facts it appears that vomiting is a complex and irregular muscular act, which may be induced by the stimulation of various parts of the internal surfaces of the body, particularly those which receive branches from the vagus nerve.

One would therefore be inclined to suppose that some afferent nerve channels exist in the vagus which bear impulses to a vomiting nerve centre and excite it, so as to cause it to send forth peculiar and irregular impulses to the respiratory, gastric, and other muscles, and give rise to their characteristic spasm.

In short, it would seem to be a reflex act, the afferent impulses of which pass to the medulla oblongata by the vagus, and the efferent impulses are conveyed by the ordinary spinal nerves to the respiratory muscles, by the vagus to the pharyngeal, laryngeal and gastric muscles, and by the fifth, seventh, and ninth nerves to the palatine, facial, and hyoidean muscles. This vomiting nerve centre must lie in the medulla, in very close relationship to the respiratory centre, with which it nearly corresponds. This centre may bring about the whole sequence of events known as vomiting when stimulated either directly by poisons, contained in the blood, indirectly through the vagus, or even from the higher centres by emotions or ideas. Section of the vagi renders vomiting impossible, as it cuts off both the commonest source of stimulus going to the centre, and also the important efferent impulses which cause the muscle coat of the stomach to contract and to open the cardiac orifice.

Movements of the Intestines.—The muscular coats are somewhat differently arranged in the small and the large intestines, but have the same general relation to each other, viz., a thin longitudinal layer lying externally, next the serous membrane, and a layer of circular fibres considerably thicker lying internally under the mucous membrane. In the large intestine the external longitudinal fibres are collected into three bands placed at equal distances one from another, which, being rather shorter than the remainder of the intestine, throw the intermediate part into a series of pouches.

It is in the small intestine that peristaltic motion of the most typical kind occurs. A wave of contraction passes from the pylorus along the circular fibres, so as to look like a broad ring of constriction progressing slowly downwards.

The longitudinal fibres at the same time contract so as to shorten the piece of intestine immediately below the ring of constriction, and also cause a certain amount of rolling movement of those loops of intestine which are free enough to move.

This motion takes place periodically in proportion to the amount and character of the contents of the intestine, the food passing over the mucous membrane being to all appearance the stimulus which normally calls forth and intensifies the action.

The activity of the peristaltic movements varies with many circumstances besides the contents of the intestines. Of these the most noticeable is the amount and character of the blood flowing through the vessels of the intestinal wall. Thus stoppage of the blood current by tying the arteries, or deficiency of oxygen and excess of carbonic acid, causes inordinate activity of the peristaltic action. Direct irritation of the serous surface of the intestine, with mechanical, chemical, or electrical stimuli also causes an increase in the movements of the intestine.

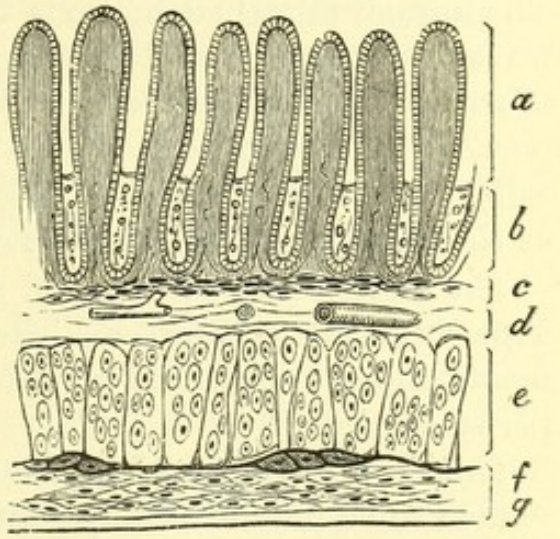


Fig. 55.—Diagram of a longitudinal section of the wall of the small intestine.

a. Villi.
b. Lieberkühn's Glands.
c. Tunica muscularis mucosæ, below which lies Meissner's nerve plexus.
d. Connective tissue in which many blood and lymph-vessels lie.
e. Circular muscle fibres cut across with Auerbach's nerve plexus below it.
f. Longitudinal muscle fibres.
g. Serous coat.

The great activity of the motion observed when the abdominal cavity of a recently killed animal is opened depends partly on the exposure to cool air, and partly on the venous character of the blood in the vessels no longer oxidised by respiration.

The irregular and impetuous action of the intestine which follows the constriction or strangulation of a hernial protrusion, probably depends chiefly on the mechanical stimulation, but also is intimately related to interference with the blood supply consequent on the pressure exerted by the constricting band. Prolonged over-work often induces immobility of the intestinal wall, and hence we find the purging and vomiting, which accompany a temporary hernial constriction, followed by inability of the intestine to propel its contents.

These points have also been proved by results of experiments on the lower animals.

The movement of the large intestines are the same as the small, but not so obvious, owing to the modified sacculated shape of this part of the alimentary canal. The contractions of the colon begin at the ileo-cæcal valve where the peristaltic wave of the ileum ceases. The normal intestinal motions thus pass in an almost uninterrupted wave from the pylorus to the end of the gut, but when special sources of irritation exist, a wave may originate in almost any intermediate part of the intestine. A reversed "anti-peristaltic motion," as it is called, only occurs as a result of some intense local stimulation, such as the strangulation of a hernia, &c.

The motion produced by the substances contained in the intestine depends on their character. The solid parts excite more rapid movements, and the more fluid portions but slightly influence the intestinal peristalsis.

Thus the solids which make their way through the pylorus are seldom to be found in the jejunum, no matter at what period after a meal the animal be killed, whereas the folds of the mucous membrane are always bathed in a fluid creamy material during the entire period of digestion, and even for a considerable time after all the food has left the stomach.

Mechanism of Defæcation.—This is a point of much importance, for the evacuation of the lower bowel is intimately connected with feelings of comfort and health, and, in illness, the insuring of its accomplishment forms an essential part of the physician's duty.

The movements of the intestine cause the various excretions and indigestible parts of the food to pass towards the sigmoid flexure of the colon, where their onward motion is checked for a time by the strong circular muscle of the rectum (called the superior, or *tertius sphincter* by Hyrtl), which does not carry on the peristaltic wave. The materials here get packed into a more or less solid mass, which is gradually augmented after each meal.

The lower outlet of the alimentary canal is closed by two distinct sphincter muscles. One thin external superficial muscle, made up of striated fibres, belongs to the perineal group, and has little influence on the closure of the anus. The deep or internal sphincter, which is much stronger, surrounds the gut for rather more than an inch (3 centimetres, Henle) in height, and is one quarter inch thick. It is made of smooth muscle, and therefore capable of prolonged

(tonic) contraction. It would appear, however, that this strong sphincter is merely a supernumerary guard to the anal orifice, but rarely called into action, for during the interval of rest between the acts of defæcation, the fæces do not come in contact with the portion of intestine surrounded by this muscle. The rectum for quite one inch above the sphincter is perfectly empty, being kept free from fæculent particles partly by a fold of the intestinal wall, and partly by the repeated action of the voluntary muscles in the neighbourhood, which by intensifying the angle that exists at this point, and flattening this inch of rectum, can squeeze back the approaching matters. Anyone familiar with the digital examination of the unevacuated rectum, knows that no fæces are met with for about two inches.

Considerable accumulation may take place in the sigmoid flexure without much discomfort ensuing, but when the rectum is distended, an urgent sensation of wanting to empty it is experienced, and the voluntary movements mentioned above, are performed by the levator ani and the neighbouring perineal muscles, with the object of preventing any substance reaching the part of the rectum immediately above the sphincter.

If the rectum be distended with fluid, the occasional anal elevation does not suffice to keep it back, and a continuous and combined action of the sphincters and levator ani, &c., is necessary to ward off the expulsion of the contents.

When the lower bowel is habitually emptied at the same hour daily—a habit which should be carefully exercised—the sensations of requirement to go to stool occur with great punctuality, or can be readily induced by the will, so that normal defæcation is reputed to be, and practically is, a voluntary act. But not completely so, for, somewhat like swallowing, the later stages of defæcation, consist essentially of a series of involuntary reflex events which we can initiate by the will, but when it is once started, are powerless to modify until the reflex sequence is completed.

Under ordinary circumstances, the evacuation of the fæces is commenced by the voluntary pressure exercised on the abdominal contents by the respiratory muscles. The diaphragm is depressed, the outlet of the air passages firmly closed, and the expiratory muscles thrown into action, while at the same moment the muscles which close the pelvic outlet relax, and allow the anus to descend, so that the inferior angle of the rectum is straightened, and a voluntary inhibition of the sphincter is brought about. This voluntary expiratory effort seldom requires to be continued for more than three or four seconds before

some fæcal matter reaches the part of the rectum just above the sphincter. When this has occurred, no further abdominal pressure is necessary (except when the masses of fæces are large and hard), for the local stimulus starts a series of reflex acts which carry on the operation. These consist of an increased peristaltic contraction of the colon and sigmoid flexure, the waves of which pass along the rectum. These waves are accompanied by synchronous rhythmical relaxation of the sphincter, which replaces its normal condition of tonic contraction.

The effect of the voluntary effort, and the amount of the abdominal pressure required, depend upon the consistence of the fæces. When quite fluid, they constantly tend to come in contact with the sensitive

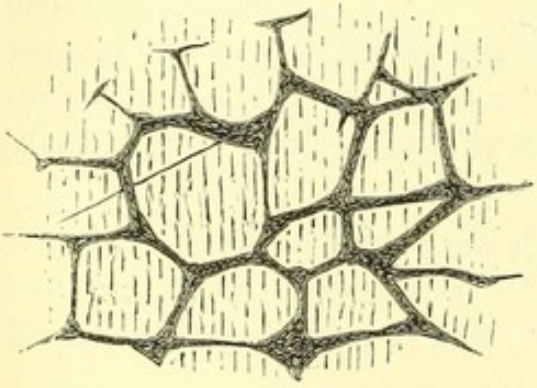


Fig. 56.—Auerbach's plexus from between the muscle coats of the intestine with low power.

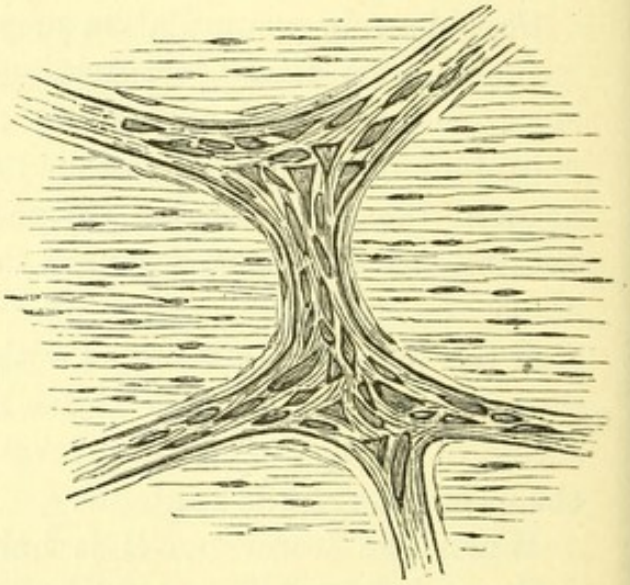


Fig. 57.—A nodal point of Auerbach's plexus under high power, showing the nerve cells.

point of the rectum, and a voluntary effort is required to prevent the reflex series of events from taking place, a momentary relaxation of the sphincter with voluntary abdominal pressure is sufficient to eject the contents of the bowel. On the other hand, when the fæces are firm, time is required in order that the slowly acting smooth muscle may pass the mass onward. In common constipation, the difficulty is to get the solid mass down to the sensitive exciting point, in which case a few drachms of warm fluid, used as an enema, may awaken the necessary reflex movements.

Nervous Mechanism of the Intestinal Motion.—Many points in the nervous control exerted over the intestinal muscles are obscure. We know that intestinal movements which are peristaltic in their nature occur in a portion of intestine removed from the body, and

thus separated from all central nervous control. We know also that there are abundant nerve elements in the walls of the intestines which have all the characters of ganglion cells, and therefore probably act as nerve centres. (Figs. 56, 57.)

With regard to these local nervous agencies, anatomists have made out two distinct sets, both of which have the form of a network of nerve fibrils studded with cell elements at their nodal points. One of these, a closely meshed plexus with flattened cords and ganglionic masses at their points of union, lies between the longitudinal and circular layers of muscle (Figs. 56, 57) forming the *plexus myentericus exterior* of Auerbach, and most probably controls the movements of these layers of muscle. The other lies internal to the

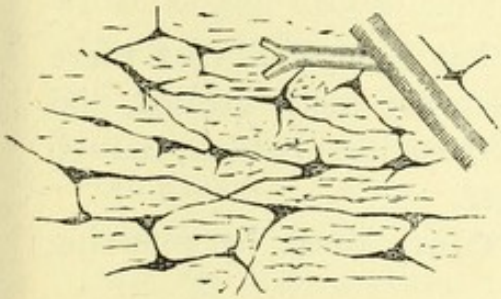


Fig. 58.—Meissner's plexus, low power.

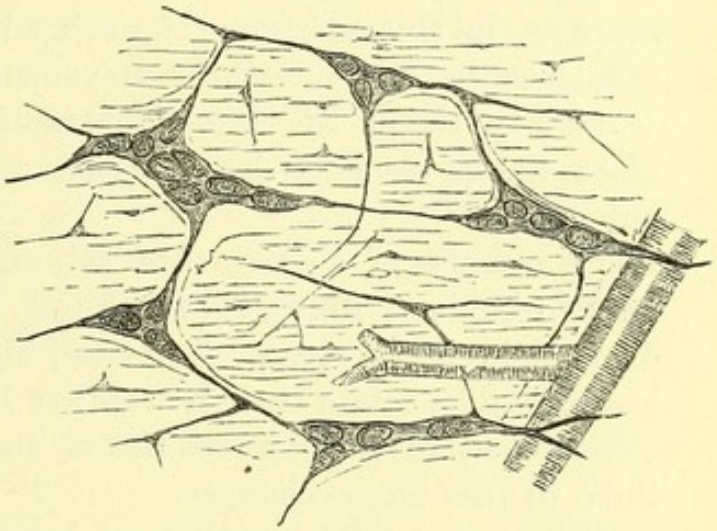


Fig. 59.—Meissner's plexus (high power), showing cells grouped at nodal points.

circular muscle, in close relation to the muscularis mucosæ, and is called the *plexus myentericus interior* of Meissner; the meshes of which are looser and more irregular, and the cords and ganglia more rounded and finer than those of Auerbach's plexus. (Figs. 58, 59.)

The blood flowing through these nerve centres in all probability acts as a sufficient stimulus under ordinary circumstances, to produce some peristaltic motions, and hence we may say that they are automatic. When food comes into the intestine it increases the flow of blood, as well as mechanically irritating the intestinal wall. The intestinal vessels remain engorged so long as the process of digestion goes on. Food seems to act more effectually than insoluble mechanical stimuli, for when insoluble substances are placed in the gut, they at first call forth active movements; but these do not last long, for the stimulus is not of itself adequate to excite prolonged

action, except it be associated with continuing congestion dependent upon other causes, such as the vaso-motor changes accompanying the general digestive process, and the absorption of the prepared food-stuffs.

With regard to the influence of other nerves, it seems to be admitted on all sides that the vagus acts as an exciting nerve, since stimulation of its peripheral part causes increased action, and it is probable that its great efferent channel for impulses is reflected through the brain.

On the other hand, the splanchnic nerves, which come from the thoracic sympathetic, are said to be inhibitors of the myenteric plexuses. This may be explained by their effect on the small vessels —which they no doubt control—causing a change in the blood supply. Be this as it may, the splanchnic seem to have considerable influence on the intestinal movements. When stimulated they commonly check the intestinal motions, but may sometimes (as when the movements have ceased after death) give rise to new movements.

On account of this double action, it has been said that there are two kinds of fibres, (1) inhibiting, which are easily excited, and during life have greater influence, and (2), exciting, which, though less excitable, retain their irritability longer.

However, most of these effects may be explained by referring them to vaso-motor changes.

With regard to defæcation, we know that a nerve centre exists in the lumbar portion of the spinal cord, which governs the sphincter, and seems to keep up its tonic contraction. This centre may be either excited to increased action or inhibited, by peripheral stimuli or by central influences from the brain.

Thus the local application of warmth causes inhibition of the centre, and thereby relaxation of the sphincter, while cold gives rise to increased central action, causing contraction of the sphincter muscle (a point to be remembered when examining or operating within its grasp). Besides the voluntary variations which we can bring about in the activity of this lumbar centre, many other central influences, such as emotions, may operate upon it. Thus terror inhibits the centre, and loosens the sphincter independently of our will.

CHAPTER VII.

MOUTH DIGESTION.

THE cavity of the mouth is lined by a bright red mucous membrane, which is continuous with the skin at the lips. It varies in structure in different parts of the buccal cavity, and in its general construction more resembles the outer covering of the body than the mucous membrane lining the alimentary tract. It consists of (1) a superficial part composed of thick stratified epithelium, the upper cells of which are flat, scaly, and tough, and are placed horizontally, while in the deeper layers the cells are soft, rounded or elongated, having their long axis perpendicular to the surface ; and (2) a deeper part composed of fibro-elastic tissue, which, over the alveoli of the teeth, is amalgamated with the periosteum and forms the dense tough gums.

The mucous membrane of the mouth is covered with papillæ which on the dorsum of the tongue attain great magnitude and variety of shape and epithelial covering. In man, three kinds are described :—(1.) Narrow pointed, *filiform.* (2.) Blunt and clubbed at the apex, *fungiform.* (3.) Broad complex papillæ, *circumvallate,* surrounded by a fossa, of which there are but a limited number (about a dozen).

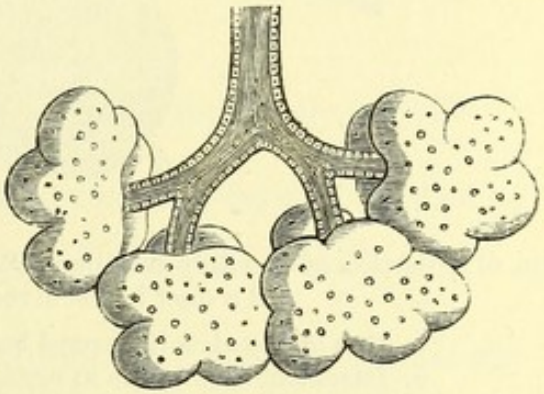


Fig. 60.—Diagram taken from a small portion of sacculated gland from Cockroach, showing branching duct and saccules.

The special secreting organs or glands, which pour their juices into the mouth, have all the same general type of structure, though they vary much in the detail as to the variety and character of their cells. They are known as the *acinous* or *sacculated* glands, from their being made up of numerous *acini,* or minute elongated sacs or tubules, arranged at the end of a repeatedly branching duct, like grapes on the terminals of the successive little branches growing

from the central stalk to form a bunch. In the glands the saccules are packed together closely around the ducts, and by mutual pressure are made to assume various shapes. The wall of the saccule is formed of a very delicate clear transparent membrane, on the outside of which are numerous flattened branching stellate cells, the branches of which anastomose one with another, and appear to penetrate the membrane in order to reach the inside of the acini.

The cavity of the little sacs is almost completely filled with large polygonal *gland-cells*, so that only a very narrow space exists in the centre. (Fig. 61.) From this space there is free communication to

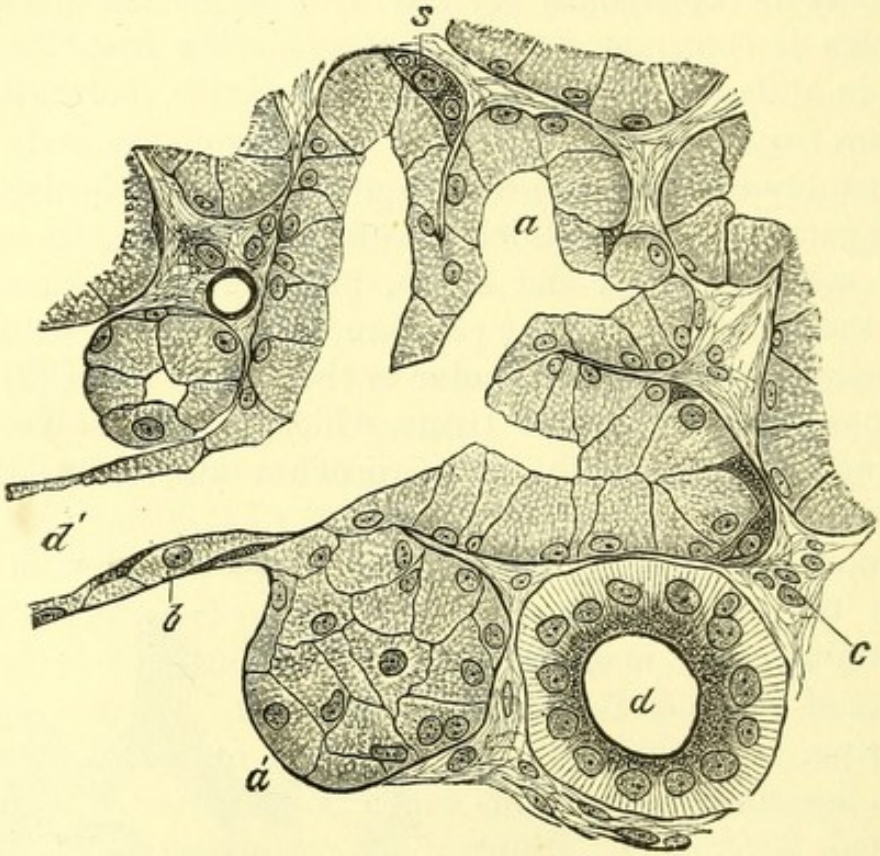


Fig. 61.—Section of the Sub-maxillary Gland of the Dog, showing the commencement of a duct in the alveoli. × 425. (Schäfer.)

a. One of the alveoli, several being grouped round the ductlet (*d'*).
b. Basement membrane in section.
d. Larger duct with columnar epithelium.
s. Half-moon group of cells.

the main duct of the gland by means of the proper ductlet of each saccule. In the saccules of a few glands, viz., some of the so-called mucous salivary glands, another kind of cell element is seen between the gland cells just described and the wall of the sac, their outer side following accurately the concave boundary of the saccule, their inner side impinging upon the gland cells. They thus acquire a more or less half-moon shape. These demilune cells will be again referred to (page 106).

Between the saccules are numerous blood vessels which branch and form a network of capillaries on the outside of each little sac. Numerous nerves are also found, which, according to some observers, have ganglionic cell-connections in the gland substance, and send terminals into the gland-cells direct.

Although this account of the nerve terminations in the secreting cells of other glands has met with doubt, it is certain that in the lower animals nerve terminals have been traced into gland-cells, and upon physiological grounds, as will presently appear, we are forced to believe that a similar connection must exist in mammalia.

The ducts are lined with short cylindrical epithelium which

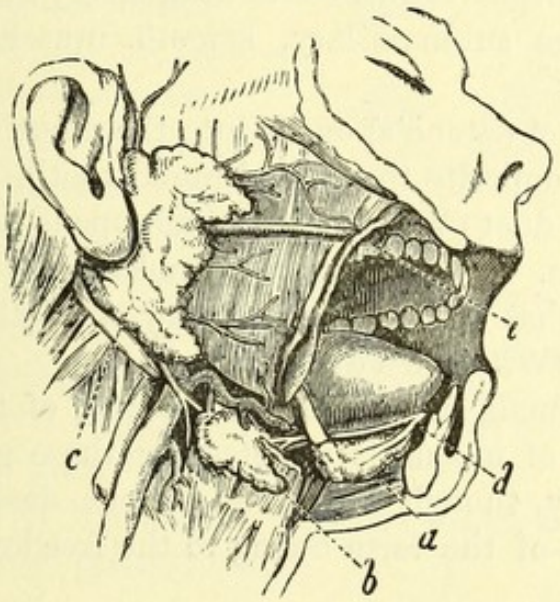


Fig. 62.—A dissection of the side of the face, showing the Salivary Glands.

a. Sublingual gland.
b. Submaxillary glands with their ducts opening on the floor of the mouth beneath the tongue at (*d*).
c. Parotid gland and its duct, which opens on the inner side of the cheek.

does not appear to have any secreting function. All the glands are made up of numerous packets of lobules bound together in one mass and united by their ducts. Each of these lobules is itself a perfect gland. The smaller mouth glands are also separable into lobules, and hence are called compound acinous glands.

The mouth glands are divided into two sets, which produce different kinds of secretion :—(1.) *Mucous glands*, which secrete *mucus*, and (2.) *Salivary glands*, which produce watery *saliva*. The functional distinction is seldom absolute, for most salivary glands have a mixed secretion, and various gradations of transition from purely salivary to purely mucous glands are met with.

The proper *mucous glands* are small, varying in size from a pin's head to a pea. They are found in groups under the mucous membrane in various parts of the mouth, and from their positions are called labial, buccal, &c. Their cells contain a clear muciginous substance.

The great *Salivary glands* are the three large glands which are known as the parotid, submaxillary and sublingual. On account of their great size they form striking anatomical objects, being large masses of irregularly arranged glandular packets, which might be spoken of as lobes to distinguish them from the smaller packets or lobules. Their ducts are of considerable size, and have strong walls made of dense fibrous tissue, containing many elastic fibres, and in one of them, the submaxillary, smooth muscle tissue has been demonstrated.

The parotid duct (Steno's) opens into the mouth about the middle of the cheek just opposite the second molar tooth. The submaxillary has also a single duct (Wharton's), which opens beneath the tongue beside the frænum. The sublingual gland has several ducts, some of which open into that of the submaxillary, and others unite to enter the mouth beside Wharton's duct.

In different animals and in different glands of the same animal a variable amount of mucus is secreted by these glands, which are all called salivary, though the parotid alone deserves the name in the strictest sense of the term owing to the freedom of its secretion from mucus.

The Characters of Mixed Saliva.

The liquid in the mouth is a mixture of the secretion of the salivary glands with that of the small purely mucous glands.

It is a slightly turbid tasteless fluid of a distinctly alkaline reaction, of 1004—1008 specific gravity, and so tenacious that it can be drawn into threads. The amount secreted by an adult human being during 24 hours varies greatly according to circumstances, and has been variously estimated by different authors, by whom the wide limits of 200—2000 grms. (7—70 oz.) have been assigned as the daily amount.

Saliva contains about ·5 per cent. of solids. Of these the greater part are organic; namely, (1.) *Mucin*, from the submaxillary, sublingual, and small mucous glands, which can be precipitated by acetic acid. To this substance the viscidity of the saliva is due. (2.) Traces of *albumin* precipitable by concentrated nitric acid

and boiling. (3.) Traces of *globulin*, precipitated by carbonic acid. (4.) *Ptyalin*, a peculiar ferment.

The inorganic constituents are salts, among which an inconstant amount of *potassium sulpho-cyanate* is found, a substance which does not exist in the blood.

There are also many morphological elements, of these the majority are accidental, being the remains of food, &c.; others are more or less characteristic; namely, (1.) *Salivary corpuscles*, which are rounded protoplasmic masses containing nuclei and coarse granules which show Brownian movements. (2.) *Epithelial scales*, from the surface of the mucous membrane of the mouth. (3.) Various forms of *bacteria*, which propagate readily amid the decaying particles of food in the mouth. No bacteria or other fungi exist in the ducts of the glands or saliva taken from the ducts with the necessary aseptic precautions.

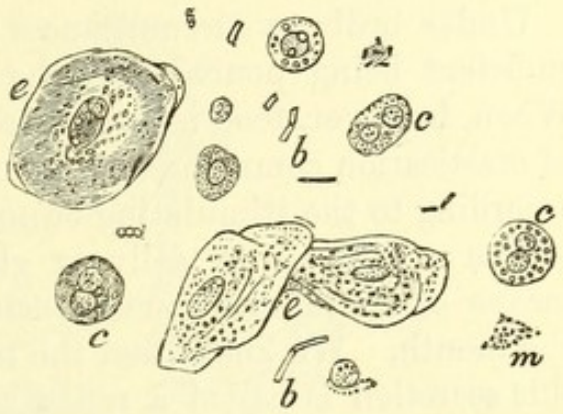


Fig. 63.—The form elements from mixed saliva from tip of tongue, showing (*e*) large irregular scaly epithelial cells, (*c*) round salivary corpuscles, several (*b*) bacteria, and (*m*) micrococci.

Collection of the Secretion.

Ordinary mixed saliva may be easily collected by chewing some insoluble material, such as a bit of rubber tubing, and collecting the fluid which the motion causes to be poured into the mouth.

The collection of the secretion of the different glands requires more delicate methods. It may be collected separately by placing a canula in the duct of each gland.

Parotid saliva obtained in this way is found to have no structural elements nor mucus, and is a thin fluid dropping easily, not capable of being drawn into threads. It contains some serum, albumin and globulin, potassium sulpho-cyanate, and ptyalin. The portion first secreted is commonly acid, and it never becomes strongly alkaline. Its specific gravity is 1003—1004. On standing it becomes turbid from the precipitation of carbonate of lime, which existed as bicarbonate.

The submaxillary secretion is more strongly alkaline than that of

the parotid; it contains structural elements and mucin, but is not so viscid as the general mouth-fluid.

The sublingual is much more viscid than either of the others, is more strongly alkaline, and contains much mucus and many salivary corpuscles.

The Method of Secretion of Saliva.

Under ordinary circumstances very little saliva is secreted, only sufficient being poured into the mouth to keep the surface moist. When, however, food is introduced into the mouth, and the process of mastication commences, the secretion goes on more or less rapidly according to the stimulating or non-stimulating character of the food.

The activity of a salivary gland is at once brought about by means of special nervous agencies when a stimulus is applied to the mouth. We know that the nervous mechanism which regulates this secretion is called a reflex act. The stimulus travelling from the surface of the mouth to the nerve centres is reflected thence to the glands. We speak, then, of *afferent nerves*, which carry the impulses to the *nerve-centre*, and *efferent nerves*, which carry them from the centre.

If we review the ordinary circumstances giving rise to a flow of saliva, there will be no difficulty in determining the nerves which act as the *afferent channels* in the simple reflex act.

Stimulation of the mucous membrane of the tongue and mouth, whether chemically, as with irritating condiments, or mechanically, as by the motions of mastication, is generally transmitted to the centre by the sensory branches of the fifth cranial nerve, which supply he mouth, and by the branches of the glosso-pharyngeal.

The stimulus of the sense of taste is sent by the nerves of that sense, mainly the glosso-pharyngeal, to the taste centre in the cortex cerebri, and from thence to the secreting centre by means of inter-central fibres.

The stimulating of the olfactory region with certain odours induces salivation through a channel of a similar kind passing along the olfactory nerve to the brain, and thence to the special salivary centre. Even in the absence of taste or smell, mental emotion may be excited by seeing or thinking of food, and may cause activity of the salivary glands, here the inter-central channel is the only one occupied in bearing the impulse to the special secreting centre.

Irritation of the gastric mucous membrane stimulates the salivary glands, as may be seen with a gastric fistula, or by the sudden flow of

saliva which commonly precedes vomiting. In this case the impulses are carried by the gastric branches of the vagus.

The stimulation of the central end of the cut sciatic is said to cause an increase in the flow of saliva, so that it would appear that even an ordinary sensory nerve can excite the centre to action. Lastly, many drugs, when introduced into the blood, cause a flow of saliva,

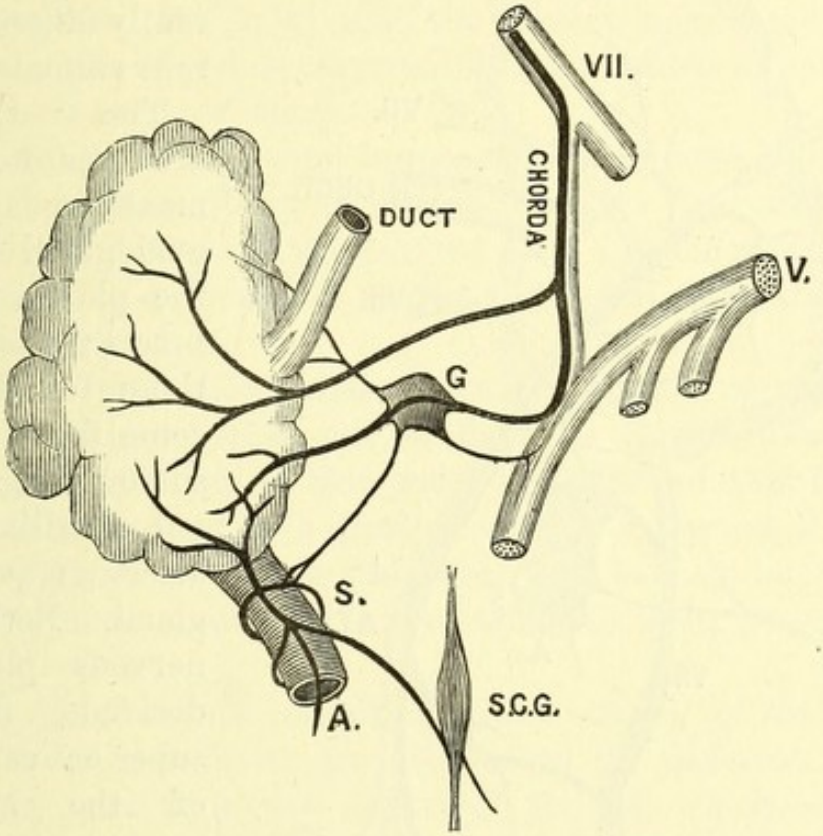


Fig. 64.—Diagram of Nerves of the Submaxillary Gland. The dark lines show the course of the nerves going to the gland.

(VII.) Portio dura; (V.) Inferior maxillary division of the fifth cranial nerve; (G) Submaxillary ganglion; (S) Sympathetic round facial artery (A); (S. C. G.) Superior cervical ganglion.

among these are pilocarpin, physostigmin, and digitalin, while atropin and daturin, on the other hand, check the action of the glands.

From this we learn that the *nerve-centre*, controlling the activity of the salivary glands, receives impulses from many distant and diverse sources, or may be influenced directly by the quality of the blood flowing through the nerve-centre itself.

The channels traversed by the *efferent impulses* going to the salivary glands have been demonstrated by experiment. In the case of the submaxillary, the route is especially distinct and instructive, so that from this gland we obtain most of our knowledge concerning the

direct influence of nerve impulses on the gland cells. This question, therefore, will be treated somewhat in detail.

There are two sets of nerves going to the salivary glands, one belonging to the *sympathetic* and the other to the *cerebro-spinal* systems, both of which have been proved to exert a certain amount of influence on the action of the glands, the share taken by each apparently differing in different animals.

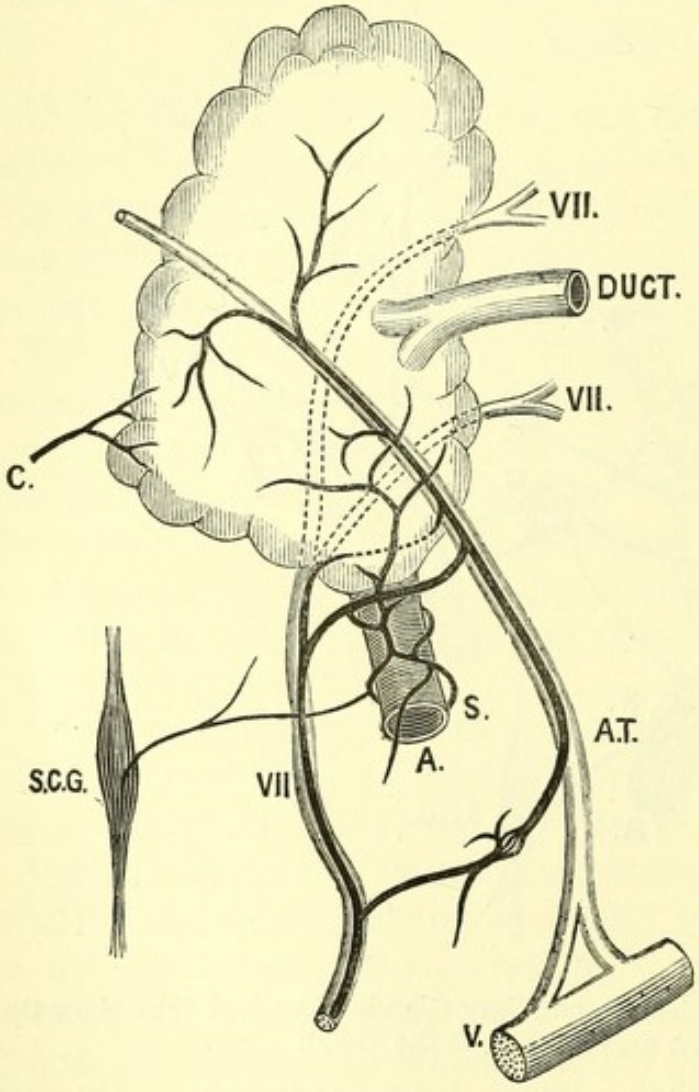


Fig. 65.—Diagram of Nerves supplying the Parotid Gland. The dark lines indicate the course of the nerves of the gland.

(v.) Inferior division of fifth nerve and its (A T) auriculo-temporal branch.
(VII.) Portio dura.
(S. C. G.) Superior cervical ganglion sending a branch to the carotid plexus around the artery.

The sympathetic branches for the submaxillary and sublingual gland come from the plexus which embraces the facial artery, those for the parotid come from the plexus surrounding the internal maxillary as that artery traverses the gland. Both of these nervous plexuses are derived from the superior cervical part of the sympathetic nerve.

The cerebro-spinal fibres for the submaxillary and sublingual glands lie in the complex nerve known as the chorda-tympani, which comes from the portio dura of the seventh, and joins the lingual branch of the fifth. They pass thence through the submaxillary ganglion to the glands.

The cerebro-spinal parotid branches pass through the lesser superficial petrosal nerve from the tympanic plexus to the otic ganglion, and thence to the auriculo-temporal nerve which sends twigs to the gland. (Fig. 65.)

I.—The effects of experimental stimulation of the *cerebro-spinal* glandular branches are, so far as we know, alike for all the glands. But owing to the greater facility with which the submaxillary gland can be reached, and its nerve isolated, research has been chiefly devoted to it, by operating on the chorda tympani and the other nerves supplying the gland.

It has been found that section of this nerve, or of the portio dura near its origin, removes the possibility of exciting the glands to action by stimulating the mouth, so that the cerebro-spinal and not the sympathetic are the channels traversed by the reflected impulse on its way to the gland from its centre.

The reflex stimuli which were supposed to be elicited through the medium of the submaxillary ganglion, probably depended on the escape of the stimulating electric current used, and the reflexion from a sporadic ganglion, such as the submaxillary, has never been satisfactorily demonstrated.

It has further been shown that direct stimulation of the chorda tympani nerve, although it be cut off from its central connections, causes a copious secretion of thin watery saliva, and this increased secretion is accompanied by a great dilatation of the small arteries going to the gland, so that a pulsation may be seen in the small veins, and the blood retains its bright arterial colour when leaving the organ.

These two chief results of stimulation, *activity of the secreting cells* and *vascular dilatation*, are distributed by different nervous agencies, as appears from the action of atropia, which stops the secretion of saliva, but does not prevent the dilatation of the vessels on stimulation of the chorda tympani; from which we conclude that its effect is restricted to a mechanism engaged exclusively in controlling the activity of the gland cells.

Stimulation of the chorda tympani causes the secretion to be carried on with great energy. The fluid was found to enter the duct with a pressure equal to 200 m.m. (about 8 inches) of mercury, while the blood pressure in the carotid artery of the animal was only 112 m.m. (about $4\frac{1}{2}$ inches) mercury; that is to say, the force by means of which secretion is driven outwards, is nearly twice as great as the pressure in the blood vessels in the gland. The secretion of saliva cannot then be a question of mere filtration, for if the physical agency—pressure—alone were acting, the saliva, if produced, would be forced into the lymph or blood vessels when the pressure in the duct exceeded that in the vessels.

The force and rate with which the secretion is produced vary with

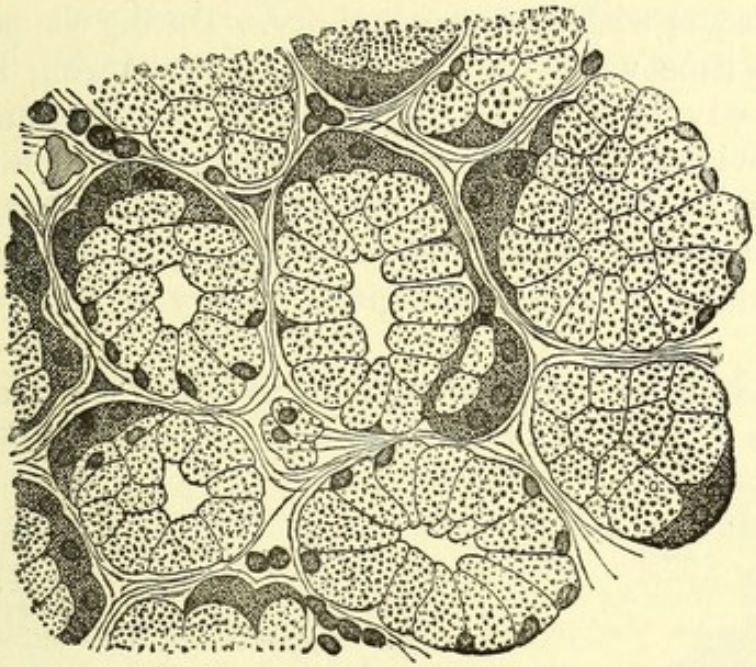
the strength of the stimulation. The flow of saliva steadily increases within certain limits as the stimulus gets stronger. It is not only the quantity of the secretion that depends on the amount of nerve impulse, but also its quality; that is to say, with a fresh gland, not wearied by previous experiment, the amount of solids in the saliva increases as the stimulus is increased, so that not only is the activity of the gland cells under the control of nerve influence, but the kind of work they perform is also regulated by the intensity of nerve impulse they receive.

It has been found that the increase in the blood flow is secondary to the secretion called forth by stimulation of the chorda tympani. This is shown by the fact that even when the blood supply is cut off by any means (strong sympathetic stimulation, ligature of the vessels, or even decapitation) an amount of saliva can be made to flow from the gland which could not have been stored up in its cells prior to the stimulation of this nerve.

II.—With regard to the influence exerted by the *sympathetic branches*, the most obvious result of stimulation of these is a contraction in the arterioles, and a consequent diminution of the amount of blood flowing through the gland. The glands look pale, and the blood leaving them is intensely venous in character; the exact opposite, in fact, to the result obtained by stimulation of the cerebro-spinal nerves. But the sympathetic has also an effect on the gland cells, as it produces an increased flow of saliva. In the dog the secretion of "sympathetic saliva" is only temporary and scanty, having high specific gravity, and being overloaded with the solids. In the cat and rabbit "sympathetic saliva" is scanty, and not thicker than the "chorda saliva" of the same animal. So far as regards the blood-vessels, the chorda is directly opposed to the sympathetic. To explain this antagonism we may either assume the existence of local nerve centres governing the muscular coats of the arterioles, and suppose that the sympathetic stimulates and the chorda inhibits the activity of these centres, or, what seems more simple, in the absence of anatomical evidence that such a centre exists, we may attribute to the arterial muscle cells themselves an automatic tonic power of contraction which can be increased by the sympathetic and diminished by the chorda tympani. It is singular that if all the nerves leading to the gland be cut, a copious secretion of watery saliva begins after some hours, and lasts for some weeks, after which the cells undergo atrophic changes, and the gland becomes reduced in size. The explanation of the appearance of this so-called "paralytic saliva" is not clearly made out. Possibly the removal of some

trophic nerve-influences induces abnormal nutritive changes which cause stimulation of the cells, and ultimately lead to their degeneration.

A



B

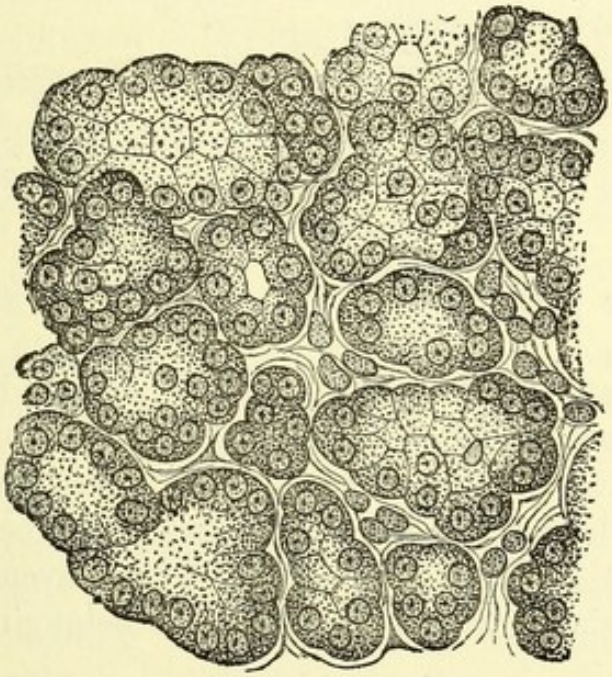


Fig. 66.—Sections of Orbital Gland of the Dog. (Heidenhain.)
(A) After prolonged period of rest. (B) After a period of activity.
In (A) the secreting cells are clear, being swollen up with mucigen, and the half-moon cells are very distinct and darkly stained.
In (B) the accumulated material has been discharged from the cells, and the alveoli are shrunken.

The histological investigation of the elements of these glands in the various stages of secretion throws considerable light

on the behaviour of the cells during their periods of activity and rest.

It is now certain that the different stages are accompanied by constant structural changes in the cells, which doubtless are intimately connected with secretory activity. During the period of rest, that is, the time when the gland is not discharging its secretion, the cells slowly undergo a change in their appearance, which is the more obvious in proportion to the ease with which the material they secrete is recognised in the protoplasm. Thus, in mucous glands, or in mucus-yielding salivary glands, the changes are conspicuous ; whilst in those which give a watery secretion they are less easily seen.

As an example we may take a mucous gland, such as the orbital gland of the dog, and follow the changes which occur in one of its

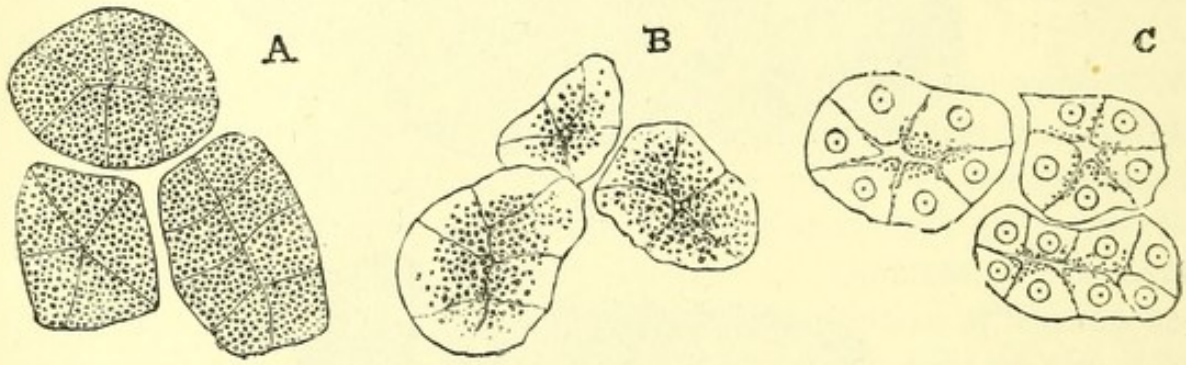


Fig. 67.—Cells of the Alveoli of a Serous or Watery Salivary Gland. (Langley.)
(A) After rest. (B) After a short period of activity.
(C) After a prolonged period of activity.

cells, during the period which may be called its cycle of activity. (Fig. 66.)

Immediately after the prolonged and active discharge of the secretion of the gland, the cells have all the characters of ordinary protoplasmic units, and the distinction between the polygonal cells and those next the wall of the acinus (demi-lune cells) is made out with great difficulty, because all the cells stain evenly with carmine, and have no special characters except those belonging to active protoplasm.

During rest certain changes gradually appear in those gland-cells which are next the lumen of the saccule. They appear to swell towards the lumen, and at the same time become clear and resist staining with carmine, their protoplasm becoming impregnated with mucus-like material (mucigen), while the demi-lune cells remain protoplasmic and stain easily, and are thereby readily distinguished from the cell in the cavity of the saccule.

If the discharge of secretion be induced either by normal reflex excitation, or by direct stimulus of the chorda tympani nerve, the cells discharge the contained specific material, some of them probably being destroyed by the act. If the active secretion be continued for some time, the cells return to their former protoplasmic state, and those which have been worn out are replaced by others from the demi-lune or marginal cells.

In the glands which do not produce any mucus the brilliant look of the cells after rest is wanting, but a corresponding change occurs. The secreting protoplasm becomes extremely granular during the resting period, and again clear after the discharge of the secretion. (Fig. 67.)

Thus it would appear that during the so-called period of rest, when little or no fluid is poured into the duct, the gland-cells are busy at their manufacturing process, diligently adding to their stock in hand in order to be ready for a sudden demand which they could not meet by merely concurrent work.

To sum up, then, we may conclude :—

I. That the manufacture of the specific materials of the secretion is accomplished as the result of the intrinsic power of the protoplasm of the gland cells.

II. That a vital process is called forth in the gland cells by the action of nerve impulses, because—(1.) The force with which the secretion is expelled cannot be accounted for by the blood pressure. (2.) The quantity and quality of the secretion is modified by the intensity of the nerve stimulation. (3.) The temperature of the blood is raised. (4.) Structural changes in the cells can be observed.

III. The normal stimulus to secretion passes from the centre in the medulla oblongata to the salivary glands along cerebro-spinal nerves.

IV. This centre for salivary secretion, which at ordinary times is moderately active, may be excited to energetic action by impulses coming from taste, smell, and ordinary sensory nerve terminals (particularly in the mouth), as well as by those which emanate from mental emotions.

Changes undergone by Food in the Mouth.

Food when taken into the mouth undergoes two processes, which are inseparable and simultaneous in action; viz., *mastication* and *insalivation*.

The mechanism of mastication has already been discussed, so far as its triturating power is concerned. In its final object of forming the subdivided food into a bolus which can be easily swallowed, it is much aided by *insalivation*, particularly in chewing dry food; and in this latter, the moistening of the particles, so as to make them adhere together, is the most necessary act of mouth digestion, and is next in importance to the subdivision accomplished by the teeth. The saliva, also, covers the bolus with a coating of viscid fluid, so that it can be more easily propelled down the œsophagus. Deglutition of solids is difficult without an adequate supply of saliva.

While in the mouth the saliva dissolves a great quantity of the more readily soluble materials, such as sugar and salt, which may be either mingled with the insoluble substances, and swallowed together with the bolus, or separately in a fluid form. Solution, then, is an important item in mouth-digestion.

In many carnivorous animals the use of the mouth-fluid is chiefly mechanical, dissolving some insignificant part of the food, and aiding mastication and deglutition. In man, however, and other animals that make use of much vegetable food, it has a chemical function, and acts on the insoluble starch, converting it into soluble sugar.

The active principle which brings about this change is *Ptyalin*. This is one of a series of *ferments* to which most of the chemical changes in digestion are due.

As a group they are remarkable for the following characters in which they differ from most chemical agents:—(1.) They effect alterations in the substances on which they act, while they themselves do not undergo any perceptible change or diminution. (2.) They exist in such small quantities that as a rule their presence can only be shown by the effects they produce. (3.) They are most active at the body-temperature, but are "killed" by that at which albumen coagulates.

Ptyalin acts on starch, and hence is spoken of as an amylolytic ferment; its action consists in causing the starch to unite chemically with one molecule of water thus:—

$$\underset{\text{Starch.}}{C_6H_{10}O_5} + H_2O = \underset{\text{Grape-sugar.}}{C_6H_{12}O_6}$$

During this process, which takes at the least a few minutes to complete, various stages can be detected: first, two substances are formed which together are commonly spoken of as dextrin; one, erythro-dextrin, which gives a red colour with iodine, and easily passes into soluble sugar; and the other, achröo-dextrin,

gives no colour with iodine, and is with difficulty converted into sugar. As it gives no colour with the ordinary test, its presence is often overlooked.

The sugar thus formed has been called *Ptyalose*, which can be converted into ordinary grape sugar (glucose) by the action of sulphuric acid. Some say the product is maltose.

The presence of starch, either in its soluble or insoluble form, is easily recognised by the blue colour given by free iodine, which colour disappears on heating to about 100° C., but reappears on cooling.

Very many tests have been recommended for the detection of sugar. The most generally applicable one is Trommer's. The liquid is made strongly alkaline with potash, and a few drops of a dilute solution of cupric sulphate is added, a clear blue solution results, which, on being raised to the boiling point, deposits an orange precipitate of cuprous oxide. Fehling's and Pavy's solutions are modifications of the above test adapted for quantitative analysis.

When yeast is added to a solution of grape-sugar, the sugar is converted into alcohol and carbon dioxide. This may be seen in an inverted test-tube. The CO_2 rises to the top, and can be used as an indication of the quantity of sugar present. Experiments may be carried out with saliva obtained directly from any of the glands, but the mixture of the secretion of all is found to be more efficacious than that of any single one. The ordinary mouth-fluid filtered serves well for ordinary experiments.

An effective glycerine solution of ptyalin may be obtained by steeping chopped salivary glands in alcohol, and then extracting for some days with glycerine and water.

The following facts must be borne in mind concerning the amylolytic action of ptyalin :—

1. The extremely small amount of the ferment required to make the fluid effective.
2. There is no appreciable diminution in the amount of ferment, so that it cannot be said to be used up in the process.
3. The action takes place most readily in alkaline solutions, such as the saliva, slowly in neutral solution, and not at all in acids of the strength of ·2 per cent. of hydrochloric acid.
4. Temperature has a marked effect on the process. Cold (0° C.), quite checks the action ; heat (75° C.) destroys the power of the ferment, which is most active at the body temperature (35°—40° C.).

5. Strong acids or alkalies destroy the amylolytic power of ptyalin.
6. The ferment has but little effect on raw starch, its cellulose coating protecting it; but it acts rapidly on well-boiled starch.
7. Ptyalin is more active in weak starch solutions, and is much impeded in its action by an accumulation of sugar.

To recapitulate, we find that the following changes take place in the mouth :—

(1) Solid food is, or should be, finely subdivided; (2) dry food is moistened, (3) rolled into a bolus, (4) and lubricated; (5) the soluble part is dissolved, and rendered capable of being tasted; (6) and part of the indiffusible starch is converted into soluble diffusible sugar by the action of a ferment called *ptyalin*.

In the short time occupied by the passage of food through the œsophagus no special change takes place in it, so we may pass at once to the gastric digestion, which will occupy the next chapter.

CHAPTER VIII.

STOMACH DIGESTION.

The surface of the stomach is covered by a single layer of cylindrical epithelial cells which also line the orifices of the numerous glands with which the mucous membrane is thickly studded. This single layer of cylindrical cells commences abruptly at the cardiac orifice of the stomach, and is marked off from the stratified squamous cells lining the œsophagus by a sharp line of demarcation. The glands of the stomach are tubes with conical orifices which often divide into two or three tubular prolongations. The outlet or orifice is covered by the common cylindrical epithelium of the surface of the stomach, and the fundus is filled with specific granular cells. The glands dip down to the delicate submucous tissue, the branching tubes lying parallel and exceedingly close together. A dense net-work of capillary blood-vessels may be demonstrated by injection to surround the tubes and closely invest the thin basement membrane which forms the boundary of the glands and the basis of attachment of the glandular cells. A close-meshed net-work of absorbent vessels also surrounds the tubules of the glands, and leads to the larger vessels in the submucous tissue.

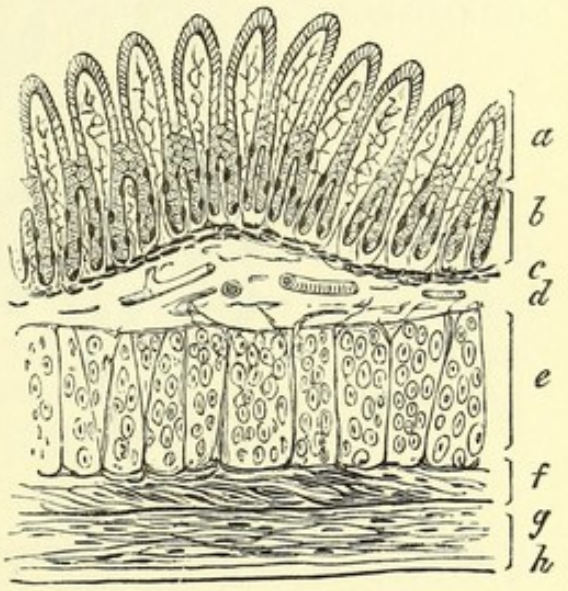


Fig. 68.—Diagram of a Section of the Wall of the Stomach.

a. Orifices of glands with cylindrical epithelium.
b. Fundus of glands with spherical and oval epithelium.
c. Tunica muscularis mucosæ.
d. Submucous tissue containing blood vessels, &c.
e. Circular, (*f*) oblique, and (*g*) longitudinal muscle coats.
h. Serous membrane.

In the cardiac end of the stomach two distinct kinds of cells are found in the deeper part of the gland tubes. Much the more numerous are small pale spheroidal cells, which occupy the lumen of the gland and form the regular cell-lining of its cavity. These cells have been called the "chief cells" (Hauptzellen), "central" or *spheroidal cells.*

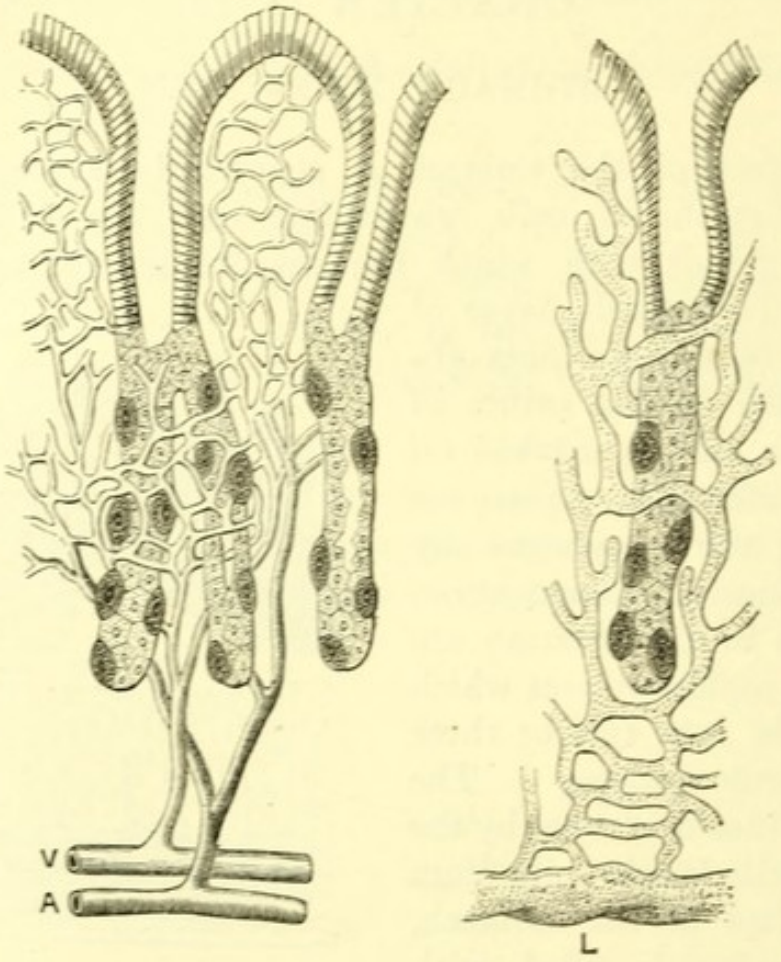


Fig. 69.—Diagram showing the relation of the ultimate twigs of the blood-vessels (V and A), and of the absorbent radicals (L) to the glands of the stomach, and the different kinds of epithelium, viz., above cylindrical cells; small pale cells in the lumen, outside which are the dark ovoid cells.

The cells of the other form are comparatively few, being altogether wanting in some of the glands. They are larger and more striking than the central or spheroidal cells between which and the basement membrane they lie scattered here and there over the fundus of the gland, making the delicate membrane bulge. They stain more easily, and have darker granules than the central cells. On account of their position they have been called "parietal," "marginal or border cells" (Belegzellen), and from their oval shape, which equally well distinguishes them from the other, "*ovoid cells.*" (See fig. 69.)

There is a different class of glands, the so-called mucous, found

chiefly near the pyloric end of the stomach, in which there is but one kind of cell throughout, and this seems to differ in character from both the varieties in the other glands, resembling rather the cylindrical epithelium covering the surface of the stomach and dipping into the conical orifices which lead to the glands.

The difference between the two kinds of glands found in the stomach, both as regards their distribution and way of branching, and the cells which line the deeper parts of the tubes, is found to vary in different animals. The difficulty of obtaining fresh specimens of the human stomach makes it still uncertain whether the same differences exist in the human subject. The varieties of opinion and drawings published suggest that various stages of gradation from one kind of gland to another are met with in the stomach of even the same animal.

Experimental research does not show decisively that the anatomical differences denote differences of function.

Characters of Gastric Juice.

The gastric juice is a clear, colourless fluid with strongly acid reaction. It contains ·5 per cent. of solids, its specific gravity being 1002. The amount secreted in the day is extremely variable, and depends upon the quantity and character of the food ; in well-fed dogs it has been estimated to be one-tenth of the body weight.

It contains :—

1. About ·2 per cent. of free hydrochloric acid in man, but in the dog considerably more. The lactic, formic, butyric, and other acids which have been found in the gastric juice probably depend on the decomposition of some of the ingesta.
2. Pepsin, the specific substance which gives the gastric juice its digestive qualities, is a nitrogenous ferment which, with the foregoing acid, acts on proteids. About ·3 per cent. is present in the secretion of the human stomach.
3. Associated with the pepsin are other less-known ferments, one of which curdles milk without the presence of any acid.
4. A variable quantity of mucus is found in the secretion of the stomach.
5. It contains ·2 per cent. of inorganic salts, chiefly chlorides of sodium, potassium and calcium.

Method of Obtaining Gastric Secretion.—Formerly attempts were made to obtain gastric juice by inducing a dog, while fasting, to swallow a sponge, and withdrawing it when saturated with the gastric secretion ; or a fasting dog, allowed to swallow insoluble materials, was killed, and the secretion collected from the stomach.

It is best obtained directly from a fistulous opening in the abdominal wall communicating with the stomach. A gastric fistula was first made accidentally in a man by injury. A case in which the surgical treatment of a gunshot wound of the stomach left a permanent fistula, allowed the gastric secretion to be carefully investigated, and proved a valuable subject for experimental research.

It is not a difficult matter to reach the stomach by making an artificial opening through the wall of the abdomen, and, having brought the serous surface of the gastric wall into firm connection with the serous lining of the abdominal wall, to open the stomach. The juxtaposition of the parts, as well as the patency of the fistula, can be secured by a suitable flanged cannula closed with a well-fitting cork. By removing the cork the gastric juice may be obtained in small quantities, and various kinds of food may be introduced through the cannula, and the changes occurring in them studied.

For experimental purposes an artificial gastric juice may be used. This can be made from the gastric mucous membrane of a dead animal (pig) by extracting the pepsin from the finely divided glandular membrane, with a weak acid (less than ·2 per cent.) or better with a large quantity of glycerine, and subsequently adding HCl to the extent of ·2 per cent.

Mode of Secretion.

The gastric juice is not secreted in large quantity when the stomach is empty, but only when the mucous membrane is irritated with some chemical or mechanical stimulus. The swallowing of alkaline saliva acts as a gentle stimulus and causes secretion, so that the surface of the stomach becomes acid. When the lining membrane of the stomach is mechanically stimulated through a fistula it becomes red, and drops of secretion appear at the point of stimulation, but the amount of secretion thus produced is very scanty when compared with that called forth by chemical irritants.

Thus ether, alcohol, and pungent condiments produce copious secretion. Weak alkaline solutions also cause secretion, but the most

perfect form of stimulant seems to be a mass of food saturated with the alkaline saliva.

In all probability the secretion of the gastric juice is under the control of a special nerve mechanism, and the way in which the state of activity follows stimulation of the part seems to point to its being a simple reflex act. However, the nervous connections (vagi and splanchnics) between the stomach and central nervous system may all be severed without any marked effect on the secretion, other than that which would naturally follow the changes in the amount of blood supply, which of course is greatly altered by cutting the vaso-motor nerves—the splanchnics. Whether this be so or not, there must be some connection with the nerve-centres, for sudden emotions check the secretions, and the sensations caused by the sight or smell of food give rise to gastric secretion.

It has been suggested that Meissner's sub-mucous ganglionic network may act as a reflex centre and regulate the secretion. But as the reflection from local ganglionic centres has not yet been definitely demonstrated, we are hardly entitled to assume that it occurs here, and since the stimulus comes into close contiguity with the secreting cells, it seems quite as probable that these elements are excited to activity by direct stimulation of their protoplasm.

As in the salivary glands, so in the gastric tubes, the cells show some structural changes which accompany with great regularity their periods of rest and activity, and therefore may be concluded to be the indications of the internal processes belonging to the production of the specific materials of the secretion.

It appears probable that the chief secretory activity resides in the small central cells, and not in the large ovoid border-cells, since no distinct changes can be seen in the latter, and the smaller gland-cells seem to contain the pepsin, for if the mucous membrane be treated with weak hydrochloric acid, these central gland-cells are rapidly dissolved by a process of digestion, while the border-cells simply swell up and become more transparent. So that the outer ovoid cells have no title to their former name of "peptic cells."

The central cells of the gastric glands are finely granular, pale, protoplasmic masses, and continue so during the time when the stomach is empty and the glands not secreting. In the earlier stages of digestion these cells swell up and become turbid and coarsely granular, and stain more readily with the aniline dyes. As the digestive process goes on the cells again diminish in size, but are found to contain a large quantity of peculiar granules, which are discharged

from the cell before its return to the ordinary state of rest. The cells are said to be rich in pepsin in proportion to their size ; when swollen during active digestion they contain much pepsin, when small, during hunger, they contain but little.

It would therefore appear that the pepsin of the gastric juice is produced as a distinct and new manufacture by the central cells of the peptic glands, and not by the other cells. Structural changes have also been followed out in the so-called mucous glands and in glands without any of the ovoid border-cells, which, taken with the fact that the alkaline secretion of the pyloric end of the stomach, where the mucous glands abound, is capable of rapidly digesting proteid if acid be added to it, tends to show that in these so-called mucous glands pepsin is also produced.

The acid is found chiefly on the surface of the stomach. The mode of its production seems distinct from that of pepsin, but is not well understood. Possibly the surface epithelial cells store up in their protoplasm and render inert the small quantities of HCl which are constantly being set free from the NaCl by the action of the newly-formed weak organic acids (lactic, &c.). The amount of HCl thus slowly accumulated in time becomes considerable and is discharged by the cells at appropriate periods.

Although the fact that the deeper part of the glands do not give an acid reaction, while the neck and orifices of the gland are distinctly acid, would support the former view, there is some reason for believing that the manufacture of acid from the alkaline blood is really an active process carried out by some glandular cells.

It has been suggested that the cell elements which produce the acid are the ovoid border-cells, from whence it rapidly passes to the orifice of the glands. This view is supported by the alkalinity of the pyloric end of the stomach where the border-cells are not found. In some animals the distinct distribution of the different cell elements and the accompanying reaction of the secretion are well marked.

Action of the Gastric Juice.

The gastric juice has in the absence of mucus no effect on the carbohydrates, and probably the amylolytic fermentation set up by the saliva is impeded, if not completely checked, by the free acid in the stomach as soon as the bolus is moistened by the gastric fluid.

Fats are not affected by the gastric juice but are simply melted in the stomach.

Upon the *albuminous bodies* the gastric digestion produces

a marked effect. The proteids being colloid bodies, cannot readily pass through an animal membrane by the process called dialysis ; it has therefore been assumed that they cannot be absorbed through the lining membrane of the stomach. They are often eaten in an insoluble form. To convert the insoluble and indiffusible albumins into a soluble and diffusible substance would obviously be a great step towards their absorption. This power is ascribed to the gastric juice. The steps of the process may be accurately followed in a suitable glass vessel, irrespective of the stomach, by using artificial gastric juice, and attending to the various conditions necessary for its action. The power of artificial gastric juice carefully prepared from the mucous membrane of an animal's stomach differs in no essential respect from that of the natural secretion in the stomach, if all the circumstances which aid the action of the gastric ferments be applied in the experiment. This action consists in a conversion of coagulated albumins into the peculiar, soluble and more diffusible form of proteid known as "peptones."

The change is not effected immediately, but certain stages may be recognised in which the two chief constituents of the gastric juice, the acid and the pepsin, seem to have special parts to play.

Shortly after the introduction of a proteid, such as boiled fibrin, into gastric fluid at the temperature of the body, the masses of fibrin swell up, become transparent, and eventually are easily shaken to pieces and dissolved.

The first step in the process seems to be brought about by the free acid, and consists in the formation of *acid albumin*. This can be shown by neutralizing the fluid during the process and thereby causing a precipitate of acid albumin. The amount of this precipitate will depend upon how far the conversion into peptone—which is not precipitated by neutralization—has progressed. Thus, in the earlier stages, nearly all the proteid used will be thrown down by neutralization, while only a comparatively small amount is precipitated in the later stages.

The formation of acid albumin may be effected with weak acid without the other constituents of the gastric juice, and therefore the preliminary step may be attributed to the unaided action of the acid ; but since this stage in the formation of peptone is constant, and the material may possibly be distinguishable from the ordinary acid albumin, it has been called *parapeptone*.

While the parapeptone is being formed by the acid, the pepsin is engaged in changing it into the final soluble, diffusible and un-

coagulable product—peptone. The pepsin by itself cannot convert proteid into peptone, as may be seen in the want of efficacy of a neutral solution of pepsin, in which neither peptone nor parapeptone is formed. In other words, pepsin solution can only change parapeptone or acid albumin into peptone. It would appear probable, however, that it possesses this property to an unlimited extent, since it undergoes no change itself, and with fresh supplies of acid a very minute quantity of pepsin can convert an indefinite amount of proteid into peptone.

The rapidity with which proteid is converted varies according to the circumstances under which it is placed as well as the kind of proteid used. If the same proteid be used the following circumstances will be found to influence the rapidity of the process :—

1. The temperature. As already stated, the *optimum* degree of heat for the change is about that of the body, 35°—40° C.

   The activity of the gastric juice diminishes when the temperature rises above or falls below this standard. The *minimum* at which it is capable of producing any effect is about 1° C. and the *maximum* is below 70° C. Boiling permanently destroys the function of pepsin.
2. The percentage of acid as well as the kind of acid has a marked effect. Though the action will go on with other acids, Hydrochloric is the most effective, and that of a strength of ·2 per cent.
3. A condensed solution of peptone or large quantities of salts in solution impede the action, a certain degree of dilution being necessary for the process. In strong solutions of proteid, the peptones must be removed by dialysis in order to allow of the continuance of the action. This occurs in the stomach by means of the blood and absorbent vessels.
4. The degree of subdivision to which the proteid has been subjected materially influences the rapidity of its conversion into peptone. The more finely subdivided the substance the greater will be the relative extent of surface exposed to the action of the digestive fluids. When large masses of coagulated albumen, such as boiled white of egg, are introduced into the stomach, the gastric fluid cannot reach the central portions, and their digestion must await the completion of that of the exterior part.
5. Motion aids the action of the foregoing factors.

All these requisites are present during normal digestion.

The temperature of the stomach is 38° C. (= 100° F.). Hydrochloric acid is present in the proportion of about ·2 per cent. As quickly as the peptones are formed they can be removed by absorption from the stomach, and thus the needful dilution is accomplished. Finally, if the mouth has done its duty, the pieces of proteid have been reduced to a pulp, composed of minute particles. These are kept in constant motion by the gastric walls, and thus are repeatedly brought in contact with fresh supplies of the digestive fluid.

There can be little doubt that the conversion of proteid into peptone is normally brought about by the pepsin, which acts as a ferment, in some way or other facilitating a process which without it is extremely difficult to accomplish. Proteids may, however, give rise to peptone without the presence of any pepsin, if they be treated with strong acids, alkalies, boiling under high pressure, putrefactive and other fermentative actions. This, together with the analogy suggested by the chemical details of the amylolytic action of saliva, which one may say depends on a molecule of water being taken up, suggests that the change of proteid into peptone is also hydrolytic, the peptones being simply an extremely hydrated form of proteid.*

So far we have found that the action of the gastric juice affects proteids alone. Its action on other constituents of food varies. *Gelatinous material* is dissolved by the gastric digestion and rendered incapable of forming a jelly ; its conversion into peptone has, however, not been established. The connective tissue of meat and adipose tissue is therefore soon removed, and the muscle-fibres fall asunder, the sarcolemma is dissolved, and the muscle-substance converted into true peptone. The delicate sheets of elastic tissue, such as basement membranes and those of small vessels, are dissolved, but larger masses of yellow elastic tissue are not affected by the gastric digestion. The horny part of the epidermis, hairs, &c., are quite unaltered, and also the mucus, which passes along the alimentary tract without change. Bone dissolves slowly, the animal

* Though proteids will not diffuse through a dead animal-membrane when distilled water is used, a fair amount of diffusion takes place if a suitable solution of common salt be employed instead of water. It must also be remembered that the gastric mucous membrane is a living active structure, and that the fluid into which the albumins have to diffuse may be regarded as a salt solution. It is therefore quite probable that a considerable quantity of albumin may be absorbed as such. The fact that peptone cannot be found in any quantity in chyle or portal blood tends to prove that the albumin does pass through the stomach wall without being changed into peptone.

part being attacked at the surface by the gastric juice and the acid slowly removing the salts.

The action of the gastric juice on *milk* is peculiar. On reaching the stomach milk is curdled by a special ferment formed in the gastric mucous membrane. This ferment, known as "Rennet," is made from the stomach of the calf, and used in the manufacture of cheese. The precipitation of the Casein (alkali albumin), which gives rise to the curdling of the milk, is not brought about by the hydrochloric acid (although the acidity would be quite sufficient), because neutralised gastric juice has the same effect. It appears that a special ferment (not pepsin) which directly affects the casein and causes its coagulation, must exist. It is not due to common lactic ferment, for though lactic acid is produced, it is formed too slowly to account for the very rapid coagulation of milk which occurs in the stomach.

The gastric juice has little effect on *vegetable food* in general, though well-masticated bread may be very materially altered, owing to the action of the saliva on the starch continuing until the mass is broken up, and the gastric juice then dissolving the proteids (gluten). The greater part of the substance of bread, however, leaves the stomach in an imperfectly digested state.

In short, the amount of change which any given form of food will undergo in the stomach will depend on the amount and exposed condition of the proteid it contains.

In recapitulating the chief events of gastric digestion, it must be remembered that while the food is yet in the mouth the secretion of the gastric juice commences, and is greatly increased by the arrival of a bolus of food and a quantity of frothy alkaline saliva. As the stomach is filled, more and more secretion is produced, and as some food is absorbed an additional stimulus is applied. Being kept in motion in a large quantity of liquid which dissolves the cases in which the food particles are contained, the bolus of food soon falls asunder and each of its ingredients is fully exposed to the action of the gastric juice. The acid reaction of the gastric fluid neutralizes the alkalinity of the saliva, so that the action of the ptyalin is hindered, and the starch granules float about quite unaffected by the pepsin or hydrochloric acid. The heat of the stomach melts the fats, and the motion breaks up the oily fluid into smaller masses. They are then mingled with the general liquid, which becomes more and more turbid owing to the admixture of starch granules, fat globules, dissolved parapeptones, and minute particles of partially digested proteids.

This dull-grey, turbid fluid is called *chyme*. The proteids (the class of food-stuffs affected by the gastric digestion) are changed more or less rapidly according as their particles are small and uncovered, or large and massed together, so that they are more or less readily reached by the gastric juice, and also in proportion to the facility with which they form acid albumin. The chyme contains but little peptones, so we may conclude that, when formed, they are rapidly absorbed, as are also the soluble sugar and ordinary fluids taken with the food. The chyme begins to leave the pylorus soon after gastric digestion has begun, some passing into the duodenum in about half an hour. The materials which resist the gastric secretion, or are affected very slowly by it, are retained many hours in the stomach, and the pylorus may refuse exit to such materials for an indefinite time, so that after causing much uneasiness they are finally removed by vomiting. However, many solid masses, unchewed vegetables, &c., escape through the pylorus when it opens to let out the chyme.

CHAPTER IX.

PANCREATIC JUICE.

The copious secretions of two of the largest glands of the body—the pancreas and the liver—are poured into the duodenum. This is the widest part of the small intestine, and the extent of the surface of its lining membrane is increased by crescentic shelf-like projections called *valvulæ conniventes*, so that its secreting follicles are numerous. In its walls are also small racemose glands not found in other parts of the alimentary tract.

The pancreas is a large compound sacculated or acinous gland, composed of numerous irregular packets of gland-tissue attached by its lateral branchlets to the main central duct. The saccules are elongated, and have the same general construction as those of the serous salivary glands already described, but they are less closely held together by the intervening connective tissue, and thus the pancreatic tissue does not show such a regular and compact arrangement on section as the salivary glands. A single layer of irregular or slightly conical secreting cells in the saccule, shows a difference of structure in its central or peripheral sides, so that an external or homogeneous zone, and an internal granular zone, may be distinguished. Each zone corresponds to one half of the cells, the clear half being next the boundary, and the granular half next the lumen of the saccule. The relative width of these zones varies with the digestive process, so that the nuclei which are situated between them sometimes appear to be in the outer clear zone, and sometimes in the inner granular zone. The outer zone colours readily with carmine, whilst the inner zone remains unstained.

The large duct which passes down the axis of the gland, receiving tributaries on all sides, is surrounded with a layer of loose connective tissue which forms its outer coat. The proper coat of the duct is composed of elastic tissue, lined by a single layer of cylindrical epithelium.

Collection of Pancreatic Juice.

From a temporary fistula the secretion of the pancreas can be obtained in sufficient quantity to determine its character and properties. It is difficult to establish a satisfactory permanent fistula: the secretion soon alters its characters, becoming thin, and losing its efficacy, probably owing to an altered or abnormal state of the gland.

An artificial pancreatic juice may be extracted by water from the gland taken a few hours after death from an animal killed during active digestion (a couple of hours after eating) and carefully minced. This extract, used with proper precautions, will have the same effect as the secretion itself.

A glycerine solution containing the active principles of the pancreatic secretion may be made from the pancreas by treating the minced gland for a couple of days with absolute alcohol, removing the alcohol, and allowing it to soak for a week in sufficient glycerine to cover it. This glycerine extract, filtered, contains but little else than pancreatic ferments.

Characters of the Secretion.—The pancreatic juice is a very thick, transparent, colourless, strongly alkaline fluid, which turns to a jelly if cooled to 0° C. It often contains about ten per cent. of solids when obtained from a temporary fistula, but it may have as little as two per cent.

Of these a considerable proportion are organic, namely:—

1. Albumin, which is coagulated by boiling.
2. Alkali albumin, precipitated by acetic acid or by adding magnesium sulphate to saturation.
3. Leucin and tyrosin.
4. Fats and soaps.
5. Salts, particularly sodium carbonate, to which it owes its alkalinity.
6. Three ferments, to which it owes its specific action on the food-stuffs.

Mode of Secretion.

The pancreas does not continue in a state of activity during the interval between the periods of active digestion. When the gland is at rest it is of a pale yellow colour, and is flaccid, but during active digestion it becomes more turgid, and assumes a pinkish colour from

the increased flow of blood. The secretion commences immediately after taking food, and rises rapidly for a couple of hours, then falls and rises again in the later hours of digestion, five to seven hours after a meal: then it gradually falls for eight to ten hours, and ceases completely when digestion is at an end. The first rise which accompanies the introduction of food into the stomach, is certainly brought about by nervous agencies of a similar nature to those of the stomach, the secretion of which follows closely upon mastication. The second accompanies the passage of the undigested food through the small intestines, and may be most conveniently explained as the result of reflex nervous stimulation of the gland-cells.

The great complexity of the *nervous mechanism* of the glands of the intestinal tract makes it difficult to ascertain the exact channels traversed by the afferent and efferent impulses. The following observations, if accurate, would tend to prove that certain inhibitory impulses pass from the stomach along the vagus to the medulla, and are thence reflected to the gland by its vaso-motor nerves. During vomiting, or when the central end of the divided vagus is stimulated, the secretion of the pancreas ceases. Section of the nerves which surround the blood vessels distributed to the pancreas causes considerable (paralytic) flow of secretion which stimulation of the vagus cannot check.

No nerve-channels have been demonstrated to carry exciting impulses direct to the glands, as the chorda tympani does to the submaxillary; but the direct stimulation of the gland itself, or of the medulla oblongata, is said to induce activity of the gland.

Structural changes in the cells during secretion:—During the period of rest, *i.e.*, no secretion flowing from the duct, and the gland being pale, the gland-cells in the acini undergo a change which may be compared with that observed in the cells of the serous salivary glands. The division of the row of cells lining the acinus, into a central granular and outer clear zone, has already been mentioned.

Immediately after very active secretion, the central granular zone is reduced to a minimum owing to the paucity of granules; and the outer zone occupies the greater part of the cell, the entire substance of which stains readily and looks like ordinary protoplasm. After rest, however, the granules re-appear, and after the lapse of a short quiescent period, the inner granular zone has again encroached on the outer, owing to the accumulation of granules which, rapidly increasing, fill the greater part of the cells, and cause them to bulge inwards and occlude the lumen of the gland. As digestion

proceeds, the cells undergo a slight change in form, so that each individual cell is more distinctly seen, and its angles are retracted, giving a notched appearance to the margin of the acinus. The blood supply during this period is much increased, red arterial blood flowing from the veinlets of the gland. At the same time the granules are diminished in number, escaping at the free central margin of the cells into the lumen, towards which they appear to crowd, leaving the outer zone once more clear and free from granules, while the lumen of the saccule and of the ducts is filled with secretion.

The examination of a single cell shows that during the period of rest with a comparatively poor supply of blood, it receives its normal

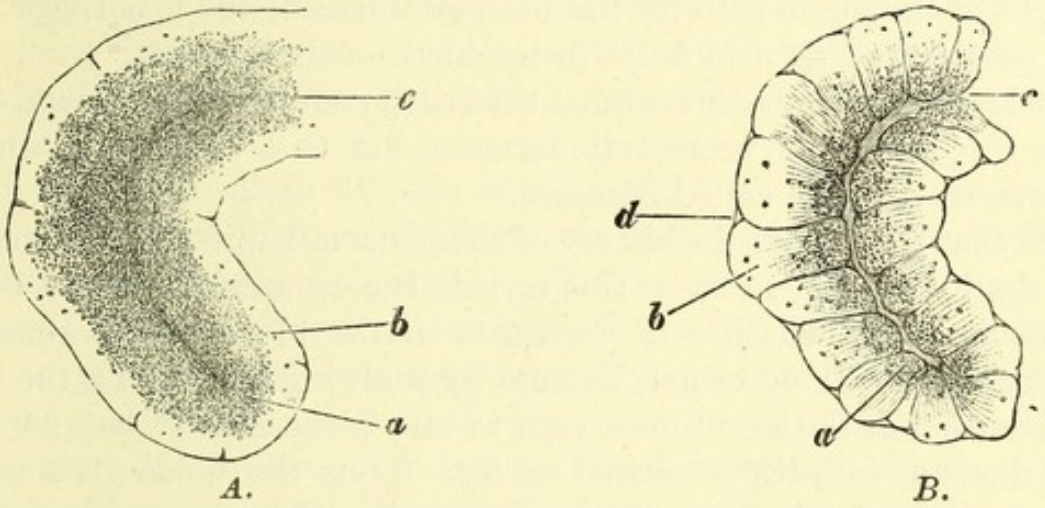


Fig. 70.—One Saccule of the Pancreas of the Rabbit in different states of activity.

A. After a period of rest, in which case the outlines of the cells are indistinct, and the inner zone, *i.e.*, the part of the cells (*a*) next the lumen (*c*), is broad and filled with fine granules.

B. After the gland has poured out its secretion, when the cell outlines (*d*) are clearer, the granular zone (*a*) is smaller, and the clear outer zone is wider. (Kühne and Lea.)

nutrition, which is accompanied by an accumulation of granules in the protoplasm next the free side of the cell. During secretion these granules are pushed out of the cell, and seem in some way to form the secretion.

It will be seen immediately that one of the most important functions of the pancreatic juice is the formation of peptone from proteid, which operation is carried out by a special ferment called *trypsin*. It has been found that this ferment can only be obtained from the active pancreas, and that the wider the inner granular zone of the cells is, the richer in ferment is the glycerine extract made from the gland, But it has also been found that if a glycerine extract be at once made

from an actively secreting, absolutely fresh gland, *i.e.*, removed from the dead animal while still warm, the extract is found to be quite inert towards proteids, while an extract made from a portion of the same pancreas which has been kept some hours after death is very active ; and a portion of the fresh pancreas pounded in a mortar with a little weak acid so as to develop the trypsin acts in an alkaline solution and forms peptone energetically.

We must therefore conclude that the special proteolytic ferment of the pancreas does not exist prior to the period at which the secretion is poured out from the gland-cells.

Although a definite relation seems to exist between the amount of granules in the active cells and the degree of efficacy of the secretion, the ferment does not appear in full force for some time after the height of the gland activity has been established, and it is likely that the presence of an acid helps in the birth of the ferment.

It has therefore been assumed that the granules of the gland-cells give rise, not to the proteolytic ferment, but to a ferment-producing substance which is called *Zymogen*.

So that if we trace the history of the pancreatic proteolytic ferment, we shall find that, so far as this trypsin is concerned, there can be no question as to whether it pre-exists in the blood and is removed thence by the gland or not, because by studying the process the final elaboration of the secretion is seen to take place after it has got into the ducts or into the intestinal cavity. Thus the blood gives nutriment to the protoplasm of the gland-cells. The protoplasm of the cells, by its intrinsic chemical processes, manufactures peculiar granules. These granules give rise, among other things, to zymogen, which in the presence of an acid begets trypsin.

Pancreatic Digestion.

The pancreatic juice is, of all digestive fluids, the most general solvent. It acts upon the three great classes of food-stuffs which require modification to enable them to pass through the barrier that intervenes between the intestinal cavity and the blood current. It changes proteids into peptones, emulsifies fatty substances, and converts starch into soluble sugar. The ferments to which its activity is due may be separately described.

I. *Action of pancreatic juice on proteids.*—The ferment which produces peptone is *trypsin*. Some of the conditions required for its perfect operation are the same as those necessary for the action of the

gastric ferment *pepsin;* namely, a certain degree of dilution, and a temperature of about 40° C. But it differs from pepsin in the most important characteristic of its action. Whilst the presence of an acid is absolutely necessary for peptic proteolysis, we find that an alkaline reaction is required for this action of the pancreatic ferment, and as the peptic peptone has to pass through preliminary stages in which it closely resembles *acid-albumin*, so the tryptic peptone is first produced from *alkali-albumin*, which has been formed as a preliminary step by the alkali of the pancreatic juice. The addition of the sodium carbonate aids the action, and indeed seems to play a part which closely corresponds to that taken by the hydrochloric acid in gastric digestion.

The change to alkali albumin and peptone as accomplished by the trypsin, is not accompanied by any swelling of the albumin such as occurs in the formation of the acid albumin in the stomach, but the proteid is gradually eroded from the surface and thus diminished in size.

Moreover, the alkali albumin is not made directly into peptone, but passes through a stage in which it resembles globulin, and is soluble in solutions of sodium chloride.

Besides these differences between the mode of action of pepsin and trypsin in producing peptones, trypsin has a peculiar power upon proteids, which has no analogue in the peptic action. While the pancreatic peptone is being produced, a further change occurs, which gives rise to the formation of two crystallizable nitrogenous bodies known as *leucin* and *tyrosin*, the former belonging to the fatty acid, and the latter to the aromatic acid group. These substances, which are commonly found together as a result of the decomposition of peptones, seem inseparable from pancreatic digestion, and increase in amount towards the later stages of the process.

The amount of peptone produced reaches a maximum in about four hours, after which the proportion of the different unknown decomposition products appears to increase at the expense of the peptone. Among these substances must be named *indol* and *skatol*, the materials from which the process of pancreatic digestion derives its peculiarly disagreeable odour.

This breaking-up of the surplus proteid food into bodies which cannot be of much utility in the economy, and which, as will appear hereafter (compare Chap. XXIII.), are but a step in the direction of their elimination, is probably an important part of the pancreatic function, as it relieves the economy of a surcharge of albuminous substances.

Small quantities of *phenol* are also found in conjunction with the above.

II. *Action on Fat.*—The action of the pancreatic juice on fats is of two kinds. (I.) Saponification.—By the action of a special ferment (*steapsin*) a small proportion of the neutral fats is split up into glycerine and the corresponding fatty acids. The acids thus produced readily unite with the alkali present, to form a little soap. The chemistry of the change will be found at p. 48, and may be shortly stated, taking olein as an example. Olein is a compound of oleic acid and glycerine. Olein in presence of this ferment and soda gives glycerine and oleic acid, and the latter combines with soda to form soap. This process materially aids in the next. (II.) Emulsification.—Which means that the fat is reduced to a state of very fine sub-division, as it exists in milk. The production of this condition is facilitated by (1), the albumin in solution; (2), the alkalinity of the fluid; (3), the presence of soap alluded to above; and (4), the motion of the intestines. This process of emulsification may be imitated by adding about one quarter volume of rancid linseed-oil to a solution of sodic carbonate and shaking in a test-tube. It will be found that the addition of a little soap and albumin will make the emulsion more perfect and more permanent.

III. *Action on Starch.*—The amylolitic power of the pancreatic juice depends on a separate ferment (*Amylopsin*). Its action seems to be identical with that of the saliva, with the exception that it is more rapid and energetic, and is said to affect raw as well as boiled starch. This power is found to exist in the extract of the gland, whether it has been removed from a fasting or from a recently fed animal, and therefore does not depend upon the gland being engaged in active secretion.

CHAPTER X.

BILE.

THE liver has two chief functions,* which are so distinct in their ultimate object that they may be conveniently described separately. One of these, namely, the secretion of *bile*, is mainly excrementitious.

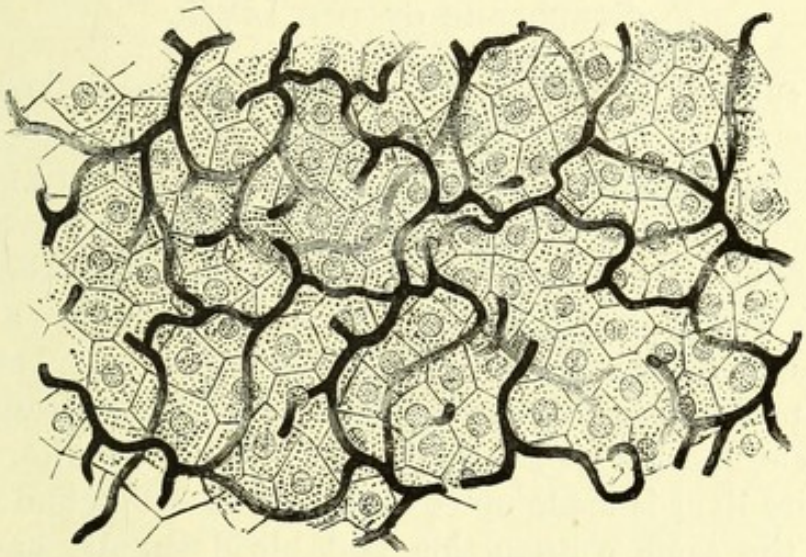


Fig. 71.—Section of the Liver of the Newt, in which the bile-ducts have been injected, and can be seen to form a network of fine capillaries.

Bile is one of the fluids connected with digestion, being poured into the intestine, and therefore is treated under this heading; but its influence upon digestion is not so great as was formerly supposed.

The other function of the liver is nutritive, consisting in the formation of *glycogen*. The glycogenic function of the liver belongs to the history of the nutrient materials after their absorption, and is of the first importance in attaining the elaboration of the blood, and will therefore be reserved for the chapter on that subject.

* The formation of urea may also be mentioned here, for there is no doubt, as will be seen later on in speaking of the excretions, that the liver has an important share in producing this substance.

Among the most striking peculiarities of the liver may be mentioned the following facts: (1) It has a receptacle, the gall-bladder, for storing the secretion until required. (2) It has a double blood-supply. It receives by the hepatic artery a small supply of fresh arterial blood as well as all that coming from the spleen, pancreas and intestinal canal, collected by the tributaries of the great portal vein, and distributed by its branches to the liver. (3) A regular network is formed by the minute channels (bile capillaries), which freely anastomose between the cells. (4) Although in the embryo, and in many animals, the liver is a compound saccular gland, the arrangement of the duct-radicles and the saccules is so modified in the higher animals and man, that their relationship is no longer apparent, and the structure is best understood by following its vascular groundwork.

Structure of the Liver.

On the surface of the liver are seen with the naked eye small rounded markings about the size of a pin's head, which give the organ a mottled appearance. This is much more striking in some animals (giraffe, bear, pig) than others, but is easily recognizable in the livers of all mammalia. These little areas are the surfaces of the *lobules* of the liver. They are surrounded by a dark red boundary, and their centre is marked by a dark spot, between these there is a paler yellowish zone. The dark parts correspond to the blood-vessels, and have a constant relation to the lobules.

The entire liver is made up of these little lobules, and each one of them has the same construction and blood supply, and therefore forms in itself a little liver perfect in all its structural arrangements, so that the description of one such unit will suffice to give an idea of the structure of the gland. For other details, anatomical works must be referred to.

The branches of the large *portal vein* and those of the small hepatic artery pursue the same course through the gland, and are enclosed in a sheath of connective tissue (capsule of Glisson), which also forms the bed of the hepatic duct and its numerous tributaries. If these branching vessels be followed to their final ramifications, they are found to pass around and between the neighbouring lobules. The branches of the portal vein in this situation receive the name of the *interlobular veins*. They anastomose freely with the terminal veinlets in the vicinity, so as to form a network round each lobule. From this a number of capillary vessels pass into the lobule,

and, lying between the gland-cells, form a network with long meshes radiating from the centre. These are the *lobular blood-capillaries.*

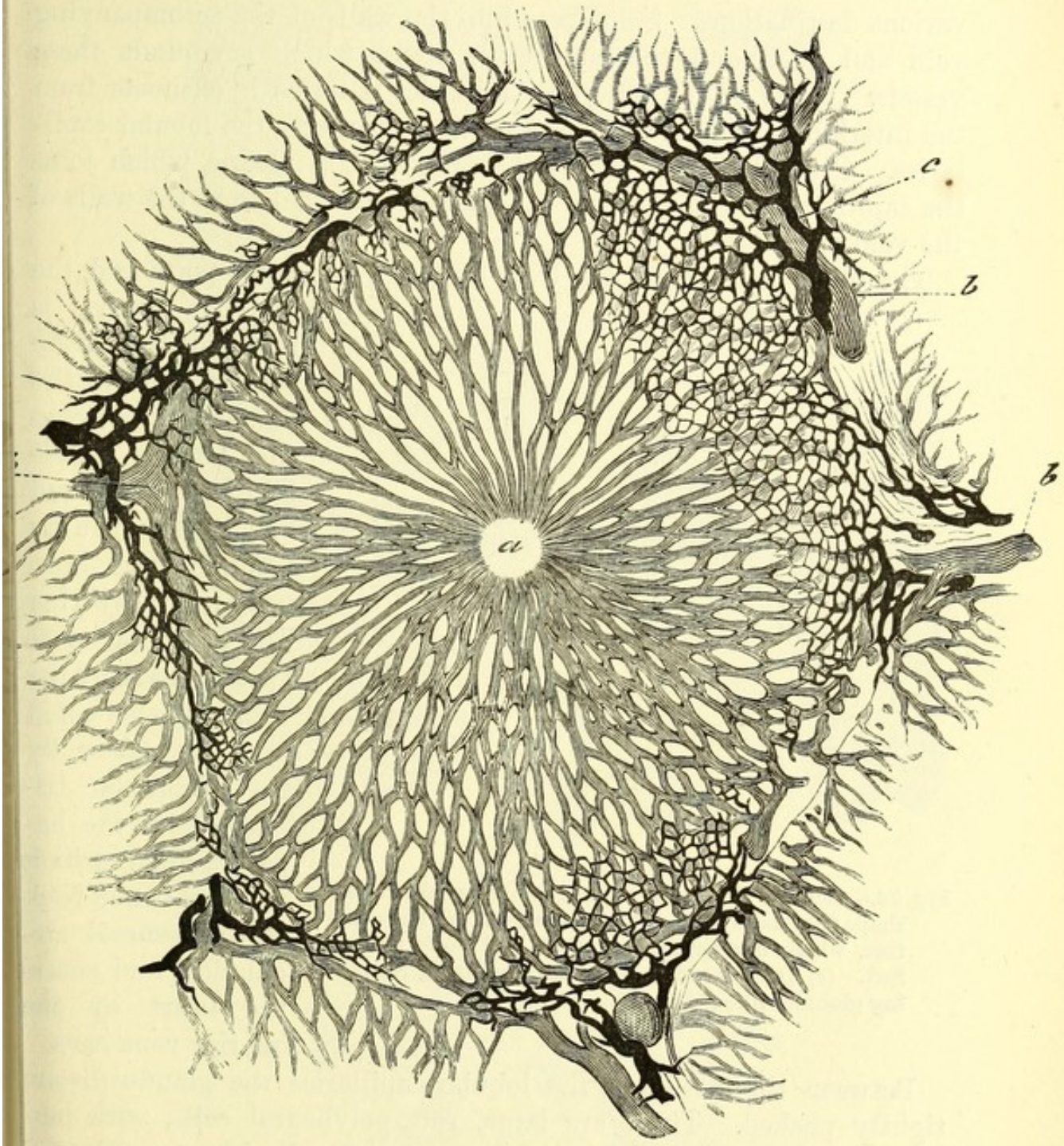


Fig. 72.—Section of Lobule of Liver of Rabbit in which the blood and bile capillaries have been injected. (Cadiat.)

a. Intralobular vein. *b.* Interlobular veins.
c. Biliary canals beginning in fine capillaries.

The vessels of this radiating capillary network become larger as they unite and converge to the centre of the lobule, where they open into a central vein which lies in immediate apposition with the gland-cells. This vein is called the *intralobular vein*, and is the radicle of

the efferent or *hepatic vein*, which carries the blood of the liver to the inferior vena cava.

The ultimate ramifications of the hepatic artery can be traced to various destinations. Some pass into the walls of the accompanying vein and duct, and the connective tissue which surrounds these vessels. Many of the arterial capillaries unite with offshoots from the interlobular venous plexus and thus re-inforce the lobular capillaries. Other branches form alobular capillary plexus, which joins the capillaries of the vena porta, together with that from the walls of the vein and duct.

The blood flowing to the liver in the great vena porta and the hepatic artery, is thus conducted by those vessels to the boundaries between the lobules (interlobular veins), and thence streams through the converging lobular blood-capillaries to the intralobular vein, and is collected from the latter by the sublobular tributaries of the hepatic vein, by which it is conducted back to the general circulation, and enters the heart by the inferior vena cava.

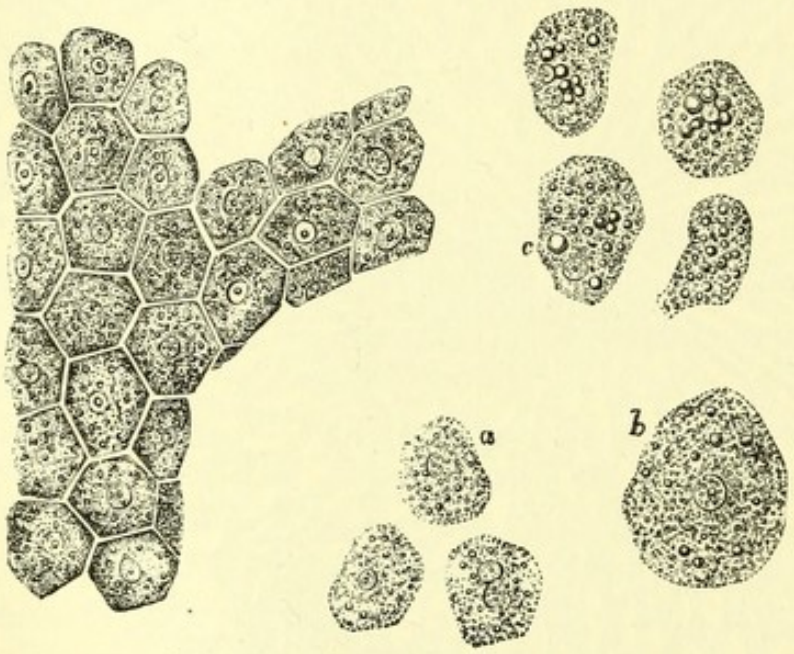


Fig. 73.—Cells of the Liver. One large mass shows the shape they assume by mutual pressure. (*a*) The same free, when they become spheroid. (*b*) More magnified. (*c*) During active digestion containing refracting globules like fat.

Between the meshes of the lobular capillaries the gland-cells are tightly packed. These are large, soft, polyhedral cells, with one, two, or even more nuclei, and no trace of a limiting membrane. Owing to the shape of the capillary meshes the cells are placed in rows radiating from the centre of the lobule towards the periphery.

The blood-capillaries are said to pass along the angles and edges of these cell-blocks so as not to come into close relation to the bile-capillaries (Fig. 71). The finely granular protoplasm of the liver-cells is capable of undergoing some slight change in form while

alive. In the protoplasm are situated varieties of granules, the commonest being bright refracting fat globules, which vary in

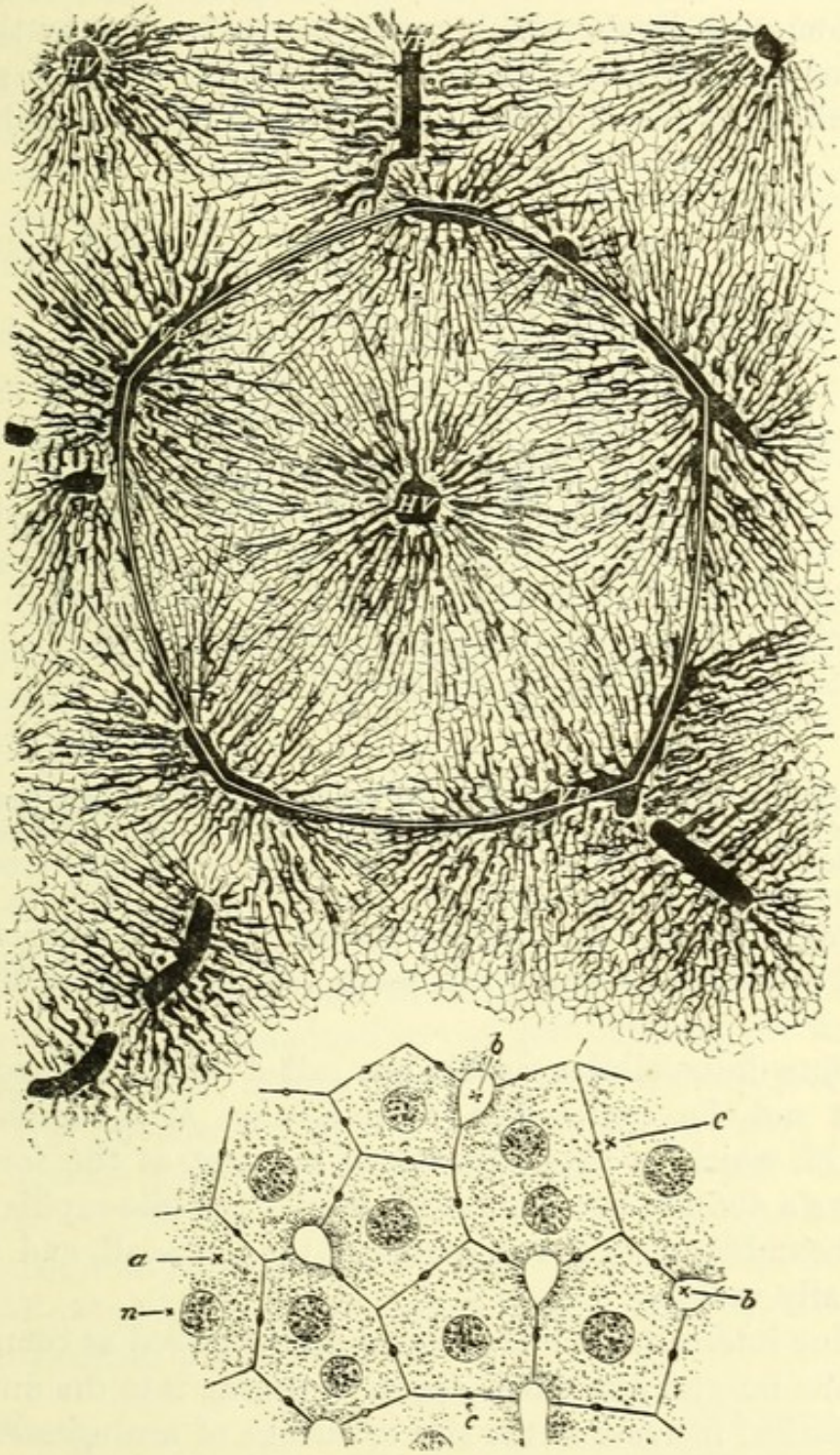


Fig. 74.—Section of injected liver showing the position of the portal branches (*interlobular veins*, VP) and radicles of hepatic veins (*intralobular veins*, HV) connected by lobular capillaries.

Below is a portion of the same highly magnified. (*a*) Liver-cell with (*n*) nucleus; (*b*) Blood-capillaries cut across passing along angles of cells; (*c*) Bile-capillaries between flattened sides of cells. (Huxley.)

amount with the different stages of digestion; others of a yellow colour, seem connected with the colouring matter of the bile; and a

third variety, less refracting and colourless, is said to be related to the glycogen.

Between the cells of the lobules there can be demonstrated very fine anastomosing canals, which appear to be formed by the juxtaposition of grooves which lie in the middle of the flat surface of two neighbouring cells. Every liver-cell is related to such a canal,

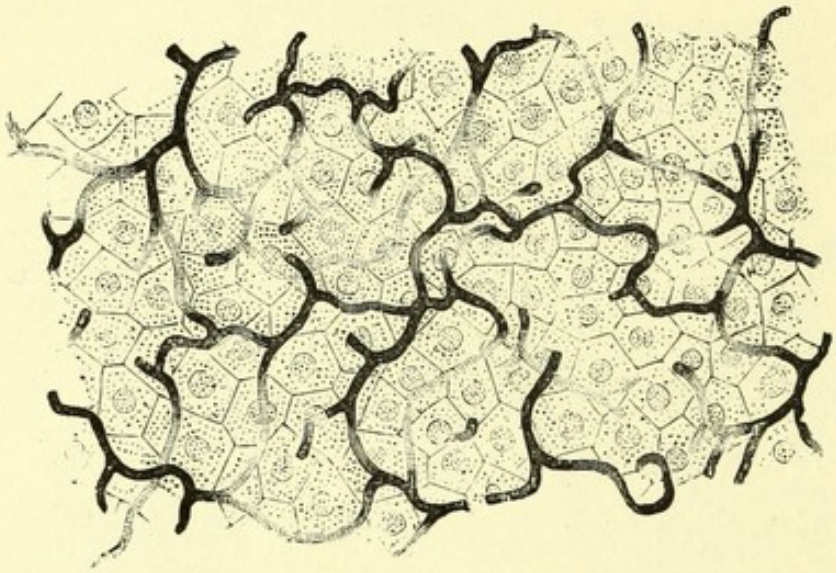


Fig. 75.—Section of the Liver of the Newt, in which the bile ducts have been injected, and can be seen through the transparent liver-cells to form a network of fine capillaries.

and consequently a very dense network with peculiarly regular polygonal meshes is present, each mesh corresponding in size to one cell.

These fine intercellular canals are called *lobular bile-capillaries*, and must not be confounded with *lobular blood-capillaries*, the diameter of which is about ten times as great as the former, and which have a definite boundary-wall, whilst the bile-capillaries have no other boundary than the substance of the liver-cell, and therefore are not really vessels.

These fine intercellular bile-passages are described as communicating with the interlobular ducts directly opening into the ducts without any marked increase in the size or change of arrangement. The interlobular ducts which follow the course of the artery and portal vein are composed of a delicate basement membrane lined with a thin layer of epithelium which in the larger vessels shows a cylindrical character. The larger bile-ducts have a firm fibro-elastic coat lined with a definite mucous membrane covered with cylindrical epithelium lying upon a vascular submucosa, in which are scattered numerous mucous glands of saccular form.

The amount of connective tissue in the liver of man and most domestic animals is very small, but in the pig, bear, giraffe, and some others, it is easily recognized around the lobules, sending delicate supporting processes between them. This connective tissue passes into the organ with the portal system of vessels forming a loose sheath derived from the capsule of Glisson, and is distributed with the subdivisions of those vessels to the various parts of the gland.

The lymphatics are known to be very plentiful, and in intimate relation to the blood-vessels.

Method of obtaining Bile.—For most practical purposes the bile from the gall-bladder of recently killed animals is sufficient. The bile pigments and cholesterin may be conveniently obtained from the gall-stones so often found in the human gall-bladder.

In order to investigate the composition of the bile as it comes from the ducts, before it has been modified by its sojourn in the gall-bladder, it is necessary to make a biliary fistula, communicating either with the gall-bladder or with the bile-duct. In this way the rate, pressure, and other points concerning the mode of secretion may be determined.

Composition of Bile.—The bile of man and carnivorous animals is of a deep orange-red colour, turning to greenish-brown by decomposition of its colouring matter. In herbivorous animals it has some shade of green when quite fresh, but turns to a muddy brown after a time. It is transparent, and more or less viscid according to the length of time it has remained in the gall-bladder. It has a strong bitter taste, a peculiar aromatic odour, and after remaining for some time in the gall-bladder it has an alkaline reaction. Its specific gravity is about 1005 when taken from the bile-ducts directly, but it may rise to 1030 after prolonged stay in the gall-bladder, owing to the addition of mucus and the absorption of some of its fluid.

The following table gives approximately the proportions of the chief constituents of bile :—

Water	85·0 per cent.
Bile-salts	10·0 „
Colouring matter and mucus	3·0 „
Fats	1·0 „
Cholesterin	0·3 „
Inorganic salts	0·7 „
	100·0

Bile contains no structural elements nor any trace of albuminous bodies.

I. The *bile-acids* are two compound acids, glyco-cholic and tauro-cholic, which exist in the bile in combination with sodium. The amount of each varies in different animals and at different times in the same animal. The bile of the dog and other carnivora contains only tauro-cholate of soda. In the ox the glyco-cholate of soda is greatly in excess. In man both are present, the proportion being variable, but the glyco-cholate greatly preponderates.

To separate these acids, bile is evaporated to one-fourth its volume, rubbed to a paste with animal charcoal to remove the pigments, and carefully dried at 100° C. The black cake is extracted with absolute alcohol, which dissolves the bile-salts. From the strong alcoholic solution after partial evaporation the bile-salts can be precipitated by ether. They first appear as an emulsion, and then form glistening crystals which are soluble in water or alcohol, but insoluble in ether.

From the solution of the two salts the glyco-cholic acid may be precipitated by neutral lead acetate, as lead glyco-cholate, from which the lead may be removed by sulphuretted hydrogen, and the acid precipitated from its alcoholic solution by the addition of water. The tauro-cholic acid may be obtained subsequently by treating with basic lead acetate.

Glyco-cholic acid when boiled with weak acids, alkalies, or baryta water, takes up an atom of water, and splits into cholic acid and glycin (amido-acetic acid). (See p. 43.)

Tauro-cholic acid, under similar treatment, splits into cholic acid and taurin (amido-ethyl-sulphonic acid). (See p. 43.)

Cholic acid occurs free in the intestines, the bile-salts being split up in digestion and tauro-cholic and glyco-cholic acids decomposed.

The non-nitrogenous cholic acid is in a great measure eliminated with the fæces, while the taurin and glycin are re-absorbed into the blood with some of the other constituents of the bile, and are again probably utilised in the economy.

No traces of these bile-acids can be detected in the blood, and there is no accumulation of them in the body after the removal of the liver; hence it has been concluded that they are manufactured in the liver.

II. The greater proportion of the *mucus* contained in the bile is produced in the gall-bladder, and there added to the bile. Some mucus comes from the mucous glands in the bile-ducts, but unless the bile has remained in the gall-bladder there is but an insignificant

amount of mucus present, as is seen when a fistula is made from the hepatic duct. The mucus passes in an unchanged state through the intestine, and is evacuated with the fæces.

III. The *bile-pigment* of man and carnivora is chiefly the reddish form called *bilirubin*. It is insoluble in water but soluble in chloroform. It can be obtained in rhombic crystals, and is easily converted by oxidation into a green pigment, *biliverdin*, which is the principal colouring matter in the bile of many animals, and is not soluble in chloroform, but readily so in alcohol. Bilirubin is supposed to be identical with hæmatoidin, a deeply coloured material found by Virchow in old extravasations of blood within the body, and hence the bile-pigment is said to be derived from the colouring matter of the blood. Probably the hæmoglobin of some red corpuscles which have been broken up in the spleen is converted into bile-pigment by the liver.

Under the influence of decomposition bilirubin undergoes a change, taking up water and forming hydro-bilirubin ; this occurs in the intestine, and the bilirubin is thus eliminated as the colouring matter of the fæces (stercobilin), which is probably identical with the urobilin of the urine.

IV. *Fatty matters*, the principal of which are lecithin, palmitin, stearin, olein, and their soda soaps.

V. *Cholesterin* ($C_{26}H_{44}O$) is an alcohol, and crystallises in clear rhombic plates, insoluble in water but held in solution by the presence of the bile salts. It can be obtained from gall-stones, the pale variety of which are almost entirely composed of it. The cholesterin leaves the intestine with the fæces.

VI. Among the *inorganic salts* are sodium and potassium chloride, calcium phosphate, some magnesia, and a considerable quantity of iron.

Tests for Bile.—The most important constituents of the bile, viz., the bile acids and pigment, may be detected by appropriate tests, which are in common practical use :—

1. Pettenkofer's test for the bile-acids :—To a fluid containing either or both bile-acids, or any solution of *cholic acid*, add some cane-sugar, and then slowly drop by drop, strong sulphuric acid. The solution turns to a cherry-red and then changes to purple. As other substances, such as albuminous bodies, give under this treatment a similar colour, in order to make the reaction a trustworthy test for bile-salts, the two characteristic absorption bands given by the spectroscope should also be observed.

The following is said to be a characteristic method :— Rinse out a porcelain capsule successively with the fluid to be tested, with weak sulphuric acid, and with a weak solution of sugar, then heat to 70° C., when the capsule turns purple.

2. Gmelin's test for the bile-pigments depends upon the fact that during the stages of oxidation the bilirubin undergoes a series of changes in colour which follow the sequence of the familiar solar spectrum. Place a few drops of the fluid to be tested on a white surface (capsule or plate), and allow a drop of nitric acid, yellow with nitrous acid fumes which make it more oxidising, to run into it; as they mingle together the rainbow-like play of colour appears. This, when watched, will be found to consist of a series of changes to green, blue, violet, red, and yellow.

   This can also be observed by allowing the acid to trickle gently down the side of a test-tube fixed in an inclined position so that it cannot be shaken : the play of colour can then be seen starting from the point of junction of the two fluids.

Method of Secretion of Bile.

The secretion of the liver varies less in the amount formed at different times than that of other digestive glands. Although the changes in the rate of its secretion are not so marked, they follow the same general rule as those of other glands connected with digestion, *i.e.*, after food is taken there is a sudden rise, then a gradual fall, followed by a second rise in the rate of secretion. This is well seen in the case of the pancreas. Want of food is said to check the secretion of bile, but only does so in a slight degree, for the more important work of the liver is continuous, as is the activity of all glands whose duty it is to eliminate noxious substances or otherwise influence the composition of the blood. At the end of a period of fasting, the gall-bladder is always found greatly distended, because the secretion has continued to flow into that receptacle, and there has been no call for its discharge into the duodenum.

The amount of bile produced by dogs is much influenced by their diet. It is very great when meat alone is consumed, less with vegetable, and very small with a diet of pure fat. As a general rule bile is more abundantly produced in herbivorous than in carnivorous animals.

The rate of secretion is much influenced by the amount of blood flowing though the organ, which probably explains the increase during digestion. Ligature of the portal vein causes arrest of the secretion, and death. After ligature of the hepatic artery the secretion continues, but soon diminishes from malnutrition of the tissue of the liver, which ultimately causes death if the entire vessel be tied.

These variations in the rate of secretion may depend on direct nervous influence, but no special secretory nerve mechanism has been discovered for the liver, and it is quite possible that the changes in the activity of the gland, which accompany the different periods of digestion, may be accounted for by changes in the intestinal blood-supply, which give rise to corresponding differences in the amount of blood flowing through the portal vein.

The force with which the bile is secreted is very small. That is to say, the pressure in the ducts never exceeds that of the blood (as is the case in the salivary glands); but, on the contrary, when a pressure of about 16mm. (·63 in.) mercury is attained, the evacuation of the bile ceases, and with a little increase of opposing force the fluid in the manometer retreats and finds its way into the blood. The low pressure which can be reached in the gall-ducts does not imply any want of secretory power on the part of the liver-cells, but merely that there exists a great facility of communication between the duct-radicles and the blood-vessels, probably through the medium of the lymphatics. This is made obvious by experiment, by which it can be shown that with a comparatively low pressure (200mm. = nearly 8 in. of water for a guinea-pig) fluid can be forced into the circulation from the bile-ducts.

This is seen also in stoppage of the bile-ducts in the human subject, when some of the bile-constituents continue to be formed, and pass into the blood, where their presence is demonstrated by the yellow colour characteristic of jaundice. The ready evacuation of the bile is a matter of great importance for health, the least check to its free exit causing the secretion to be forced into the circulating blood instead of into the gall-passages. Under normal circumstances, the large receptacle of the gall-bladder being always ready to receive the bile, ensures its easy exit from the ducts, but the forces which cause its flow are extremely weak. The smooth muscle in the walls of the duct seem rather for the purpose of regulating than aiding the flow.

When food from the stomach begins to flow into the duodenum, the muscular coat of the gall-bladder contracts and sends a flow of bile into the intestine, which action is doubtless brought about by a reflex nerve impulse, for it is only when this part is stimulated that

the bile flows freely from the bladder. The acid gastric contents seem to be the most efficacious stimulus.

In the human subject the quantity of bile secreted has been found to be about 600 cc. (21 oz.) per diem in cases where there were biliary fistulæ. This would equal about 13 grms. per kilo of the body-weight.

In the guinea-pig and rabbit, it has been estimated to be about 150 grms. per kilo body-weight.

Functions of the Bile.

1. *Neutralising and precipitating acid peptones.* — When the acid contents of the stomach are poured into the duodenum and meet with a gush of alkaline bile, a copious cheesy precipitate is formed which clings to the wall of the intestine. This precipitate consists partly of acid albumin (parapeptone) and peptones thrown down by the strong solution of bile-salts, and partly of bile-acids, the salts of which have been decomposed by the hydrochloric acid of the gastric juice. With the bile-acids the pepsin is mechanically carried down. Thus, immediately on their entrance into the duodenum the peptic digestion of the gastric contents is suddenly stopped not only by the precipitation of the soluble peptones and the shrinking of the swollen parapeptone, but also by the removal of the pepsin itself from the fluid, and the neutralisation of the gastric fluid by the alkaline bile.

By thus checking the action of the gastric ferment the bile prepares the chyme for the action of the pancreatic juice.

2. *As a stimulant*, the bile is of considerable use, for it excites the muscles of the intestine to increased action, and thereby aids in absorption and promotes the forward movement of food, and more particularly of those insoluble materials which have to be evacuated per anum. This stimulation may amount to mild purging.

3. *Moistening and lubricating.*—The bile adds to the ingesta an abundant supply of fluid and mucus, much of which passes along the intestine to moisten and lubricate the fæces and facilitate their evacuation. In cases of jaundice, or when the bile is removed by a fistula, the fæces are hard and friable, and with difficulty expelled, owing to the deficient fluid and mucus, as well as to the weaker peristaltic movements.

4. *As an aid to absorption.*—The bile having some soap in solution has a close relationship to both watery and oily fluids, and possibly on this account, as well as owing to a peculiar power possessed by the

bile-salts, a membrane saturated with bile allows an emulsion of fat to pass through it much more readily than if the same membrane were kept moistened with water. This can be seen experimentally with filter-paper.

5. *As excrement.*—Although much of the bile is reabsorbed from the intestinal tract into the blood, and again used in the economy, some of its constituents pass off with the fæces, and are no doubt simply excrementitious matters that must be got rid of. Thus all the cholesterin, mucus, and colouring matter are normally eliminated, and a considerable quantity of the bile-acids are split up, the cholic acid being found in the fæces.

6. *Emulsification of fats.*—The bile has some share in forming an emulsion, but far less than the secretion of the pancreas; however, the mixed secretions are probably more efficacious than either separately, from the presence of the free fatty acids, which form soaps and aid in forming the emulsion.

7. *As an antiseptic*, bile has been said to have some function to perform. Possibly it restricts the formation of certain of the bye-products, such as the indol resulting from pancreatic digestion; but it is certainly not *antiseptic*, since bacteria abound and thrive in it and in the duodenum.

CHAPTER XI.

FUNCTIONS OF THE INTESTINAL MUCOUS MEMBRANE.

Two distinct varieties of glands are found in the small intestine. Those known as Brunner's glands, are localised to the submucosa

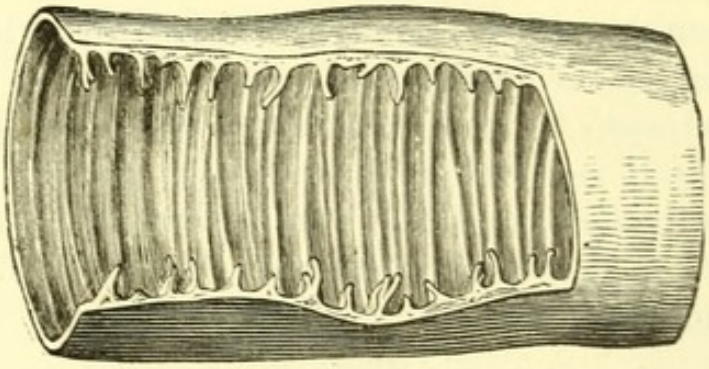


Fig. 76.—Portion of the Wall of the Small Intestine laid open to show the valvulæ conniventes. (Brinton.)

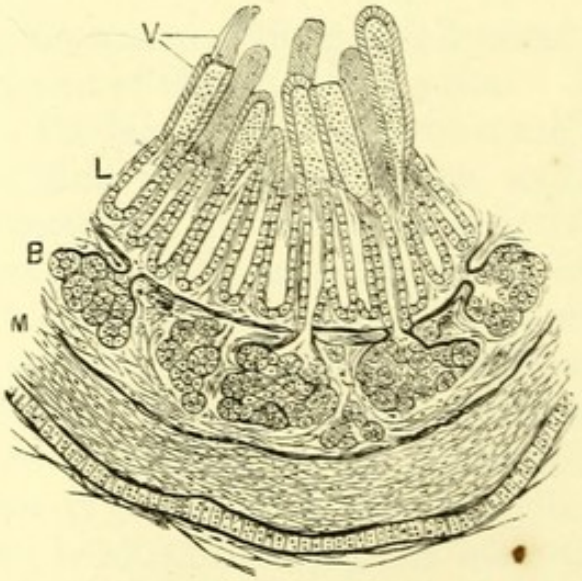


Fig. 77.—Drawing of transverse section of the duodenum showing Brunner's Glands (B) opening into Lieberkühn's follicles (L), (V) villi, (M) muscular coats.

of the duodenum; they are insignificant in number when compared with the second variety, called Lieberkühn's glands, which are

distributed over the entire intestinal tract and are closely set in the mucous membrane.

Brunner's glands form, in some animals, a dense layer in the submucous tissue of the beginning of the duodenum; they are small

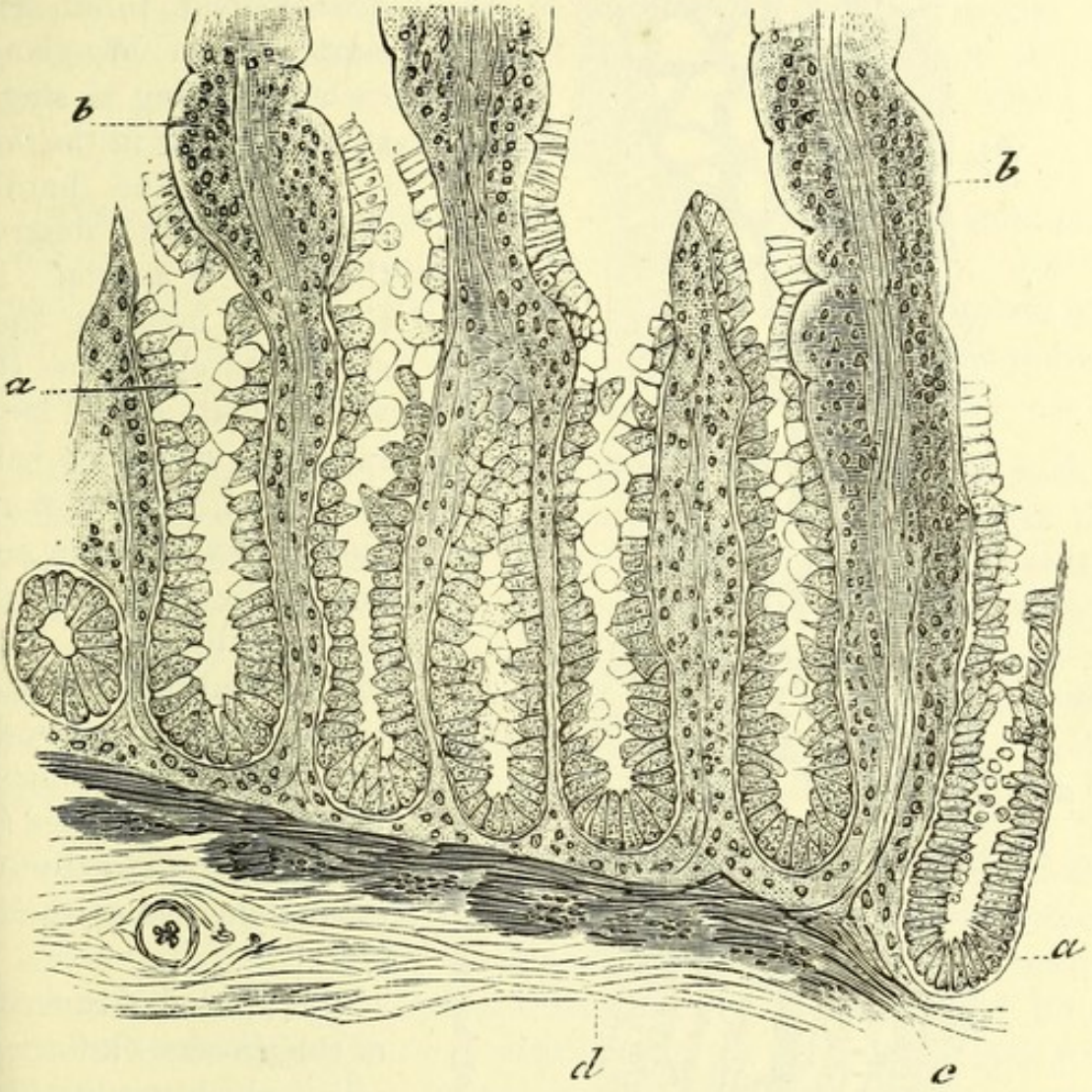


Fig. 78.—Section of the Mucous Membrane of small intestine, showing Lieberkühn's follicles (*a*) with their irregular epithelium and the villi (*b*) passing out of view; (*c*) Muscularis mucosæ; (*d*) Submucous tissue. (Cadiat.)

branched saccular glands resembling mucous glands in structure. Owing to their small size the secretion cannot be obtained in sufficient quantity to make satisfactory experiments in respect to its properties. It is said to dissolve albumin and to have a diastatic fermentative action, so that probably the secretion is analogous to that of the pancreas, as Brunner originally supposed. The quantity of fluid secreted by these glands is so small that its existence is not taken into account in speaking of the intestinal juice, by which is

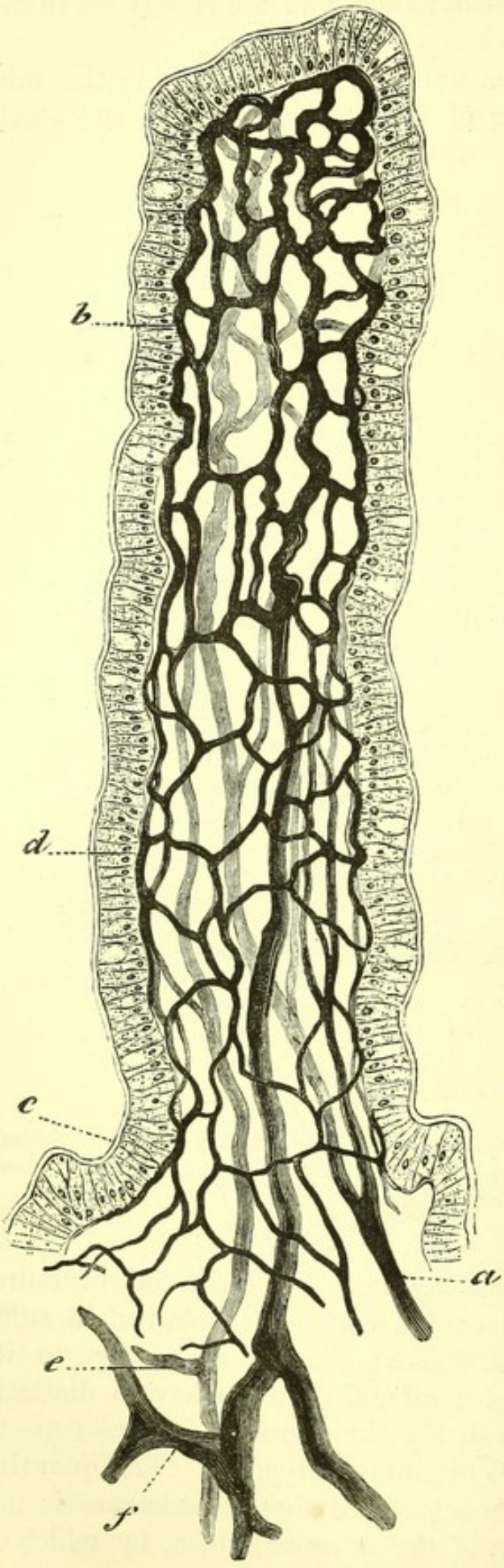


Fig. 79.—Villus with the capillaries injected showing their close relation to epithelium, some of the cells of which are distended with mucus. (Cadiat.)

meant the fluid poured out by the innumerable short tubes or follicles of the intestine.

These *Lieberkühn's follicles* belong to a very simple form of gland, each one being a single straight cavity in the mucous membrane hardly deep enough to deserve the name of a tube. In the small intestine they are set as closely as the villi permit. In the large intestine, where the villi are absent, they are more closely set and are also deeper (Fig. 78). They are bounded by a thin basement membrane which is embraced by a close capillary network of blood-vessels, and are lined by a single layer of cylindrical or spherical epithelial cells.

The epithelial covering of the processes known as villi, which are studded all over the mucous membrane of the small intestine, produce some mucus.

METHOD OF OBTAINING INTESTINAL SECRETION.—Considerable difficulty has been found in obtaining the proper intestinal juice free from admixture with the secretions of the liver and pancreas which

are carried along and mixed with it. A short portion of the small intestine has been successfully isolated from the rest without injuring the mesentery or its blood-vessels. One of the extremities of the isolated portion was closed, and the other was retained by sutures at an opening in the abdominal wall. The cut ends of the remainder of the intestine were at the same time united, so that the continuity of the alimentary tract was preserved. Thus, a limited piece of gut formed a cul-de-sac from which the fluid could be collected through a fistulous opening.

Characters of the Secretion.—The liquid obtained from such a fistula is thin, opalescent and yellowish, with a strong alkaline reaction and a specific gravity of 1011. It contains some proteid and other organic material, a ferment and inorganic salts in which sodium carbonate preponderates.

Mode of Secretion.—The secretion flows slowly from such a fistula but the amount increases during digestion, showing that the secretion of the intestine is under the control of some nerve centre which can call the entire tract into action when one part is stimulated. The local stimulation of the mucous membrane makes it red, and causes it to pour out a more abundant secretion. Beyond this little is known of the nervous mechanism or the local cell-changes which accompany the formation of the secretion.

Functions of the Intestinal Juice.—All the properties of the secretion of the pancreas have been accorded to the intestinal juice. It is said to have a ferment, capable of being extracted with glycerine, which can convert cane sugar and starch into grape sugar, and bring about lactic fermentation. It dissolves fibrin very slowly and still less easily other proteids. It is also said to emulsify fats.

The observations as to its digestive properties are discordant, for experiments have given opposite results in different animals, and in the hands of different persons even in the same animal. From the foregoing account of the intestinal secretions it may be seen that the changes which the various kinds of food undergo on their way through this part of the alimentary tract are numerous; a short review may therefore be useful.

When the acid gastric chyme escapes into the duodenum a flow of bile takes place from the gall-bladder, and at the same time the secretions of the pancreas, Brunner's glands, and Lieberkühn's follicles are poured copiously into the intestine. The bile meeting with the turbid fluid chyme causes it to change to a soft cheesy

granular mass, the appearance of which depends chiefly on the precipitation of the peptones and shrinking of the parapeptone. The pepsin is rendered powerless, both it and the bile acids being carried down with the precipitate. Gastric digestion is thus arrested and the onward flow of the fluid chyme checked. As the alkaline pancreatic and intestinal juices meet this semi-fluid cheesy mass the conversion of starch into sugar proceeds rapidly, even the raw starch granules being changed. The small oil globules come in contact with the alkaline mixture of bile and pancreatic juice. The pancreatic ferment *steapsin* splits up some of the fat separating the fatty acid from the glycerine radicle. Some of the soda of the bile salt is substituted for the latter, and uniting with the fatty acid forms a soap. In such a mixture as this—an alkaline fluid with proteid and soap in solution—a fine emulsion is readily formed, as can be seen by adding sodium carbonate to some rancid oil. The free acid (the cause of rancidity in the oil) unites with some soda to form a soap which in the alkaline mixture enables the oil to be converted into an emulsion by even slight agitation, so that the pancreas, by setting the fatty acid free, and the bile possibly by contributing some soda, aid one another in giving rise to a definite but small amount of soap.

The precipitated parapeptone and peptone and the finely divided proteid are presented to the pancreatic juice in a form which it can easily attack, and thus the conversion of proteid into peptones in the small intestine goes on rapidly.

How far the peculiar action of trypsin on proteids, converting them further into leucin and tyrosin, goes on in normal digestion is not known, but it is probable that the production of these bodies is increased with the over-abundant ingestion of proteid or a purely meat diet, and is then useful as a means of preventing the injurious effects of too great proteid absorption.

The gastric chyme is therefore completely changed in the duodenum, and in the other parts of the small intestines we find in its stead a thin creamy fluid which clings to the mucous membrane, coats over its folds (valvulæ conniventes) and surrounds the long villi of the jejunum, &c. This intestinal chyme is the form in which the food is presented to the mucous membrane for absorption. It resembles somewhat by its whiteness the fluid called chyle which flows in the lacteals, and formerly was considered to be identical with it. This creamy lining is the chief material found in the upper part of the small intestine, the coarser parts of the food being hurried onwards by peristaltic action to the large intestine.

In the large intestine the secretion of the long closely-set Lieberkühn's follicles is the only one of importance. Its reaction and that of the mucous membrane is alkaline, but the contents of the colon are acid owing to certain fermentative changes which go on in this part of the intestine.

Of the changes brought about in the large intestine by the agency of the digestive juices we know but little. Judging from the large size of the cœcum and colon in herbivorous animals, we are prompted to conclude that vegetable substances, possibly cellulose, may be dissolved here, but we do not know how this is accomplished.

Although devoid of villi, the large intestine can certainly absorb readily such materials as are in solution. As the insoluble materials pass along the small intestines the supply of fluid is kept up to about the same standard, the absorption and secretion being nearly equal; but in the large intestine, the absorption of the fluid so much exceeds the secretion that the undigested materials are gradually deprived of their fluid, and are converted into soft solid masses which pass on to be added to the fæces.

Owing to its absorbent power the large intestine forms a ready channel by which materials can be introduced into the system in cases in which the stomach is too irritable to retain food.

The quantity of fæces evacuated in the day depends upon the kind of diet, being greater with a vegetable than meat diet, averaging about 150 grammes a day (60-250 grms.). This amount may be greatly increased by partaking largely of indigestible forms of food. The more rapid the passage of the ingesta through the intestine the greater is the amount of fluid remaining with the fæces, so that any stimulant to the intestinal movements reduces the consistence of the fæces and facilitates the evacuation. The fœtor depends in a great measure on the presence of indol, which is an outcome of pancreatic digestion, and also upon the presence of certain volatile fatty acids. The colour depends upon the amount of the bile pigment and the degree of change the latter has undergone.

The fæces are composed of (1) the undigested parts of the food, and (2) the useless or injurious parts of the secretions of the various glands. In the first category we find perfectly indigestible stuffs such as yellow elastic tissue, horny structure, portions of hairs from animal food and cellulose woody fibre and spiral vessels from plants, and also masses of digestible substances which have been swallowed in too large pieces to be thoroughly acted on by the secretions. All forms of food may thus appear in the fæces, but vegetable substances are most conspicuous.

In the second category we find a variable quantity of mucus and the decomposed colouring matter of the bile, together with some cholic acid, cholesterin, &c.

A few inorganic substances are found, mainly those which diffuse with difficulty, as calcium salts and ammonio-magnesium phosphate.

PUTREFACTIVE FERMENTATIONS IN THE INTESTINE.—With the air and saliva which are swallowed mixed with the food, large numbers of the lower organisms existing in them are introduced into the alimentary canal.

The effect of these organisms is to produce certain fermentative changes quite distinct from the action of the special ferments of the digestive fluids.

This is proved by the composition of the gases found in the intestine. Atmospheric air only is introduced from without, and this is not found in any part of the alimentary tract, the oxygen soon being absorbed and the nitrogen left, while a quantity of carbonic anhydride and hydrogen from the fermentation of the sugar are set free, lactic and butyric acids being produced at the same time.

Indol and skatol are also formed by putrefactive fermentation of the leucin and tyrosin.

It is in the large intestine that putrefactive fermentations have greatest effect, the acid reaction being caused by the various acids thus produced.

With regard to the interesting question, why the digestive juices do not dissolve the tissues of the organs in which they are contained, we cannot speak positively. We can no longer say that the "vital principle" has a protective influence, for we know that the fact of a tissue being alive is not sufficient to ward off the digestive action of the alimentary juices. The limb of a living frog is digested when introduced through a fistula into the stomach of a dog; and when the intestinal juice trickles from a fistula the neighbouring skin, the snout, and the tongue of the animal soon become eaten away owing to its licking the fluid, which rapidly digests these parts so as to destroy the skin and even expose the blood-vessels.

We can however modify John Hunter's statement that the resisting power was associated with the life of the structures, by saying that it is not the property of an abstract "vital principle," but a special resisting power dependent upon the specific character of the vital processes of those textures which manufacture and are habitually exposed to the influence of the juices.

CHAPTER XII.

ABSORPTION.

THE nutritive materials must be distributed to the textures and organs in order that the food-stuffs, when altered by the various processes described under digestion, may be of any use to the economy. For this purpose they must pass through the lining membrane of the alimentary canal and gain access to the blood which is the common mode of intercommunication between the various parts of the body.

The nutrient part of the food has then to be *absorbed* out of the alimentary canal by the surrounding tissues, and mixed with the general circulating fluids, lymph and blood.

But the blood is separated from the intestinal contents by barriers, which, as far at least as the blood is concerned, is impassable, although it exerts considerable pressure, and thereby tends to escape from the blood-vessels.

The question then arises—How does the elaborated chyme make its way through this barrier, which is sufficient to prevent the flow of blood into the intestinal tract?

The general answer is easily given, viz. :—the blood cannot pass through an animal membrane. But this is not a satisfactory solution of the question, for under certain abnormal circumstances, the blood does pass through the wall of the vessels, and normally the plasma escapes from the capillaries into the tissues, in order to nourish them. We must further remember, in considering this point, that the wall of the vessels and the membrane lining the intestine are both made up of living cells which are endowed with a capability, co-incident with their lives, of controlling any passage through or between them. Some of these cells, which we might call secreting agents, do allow, or rather cause a passage of fluid from the blood to the intestinal cavity, and, as we shall presently see, others of them induce a passage of the nutritious materials from the intestinal canal into the surrounding tissues.

In order clearly to understand the method by which absorption is accomplished, it is necessary to have some idea of the absorbent

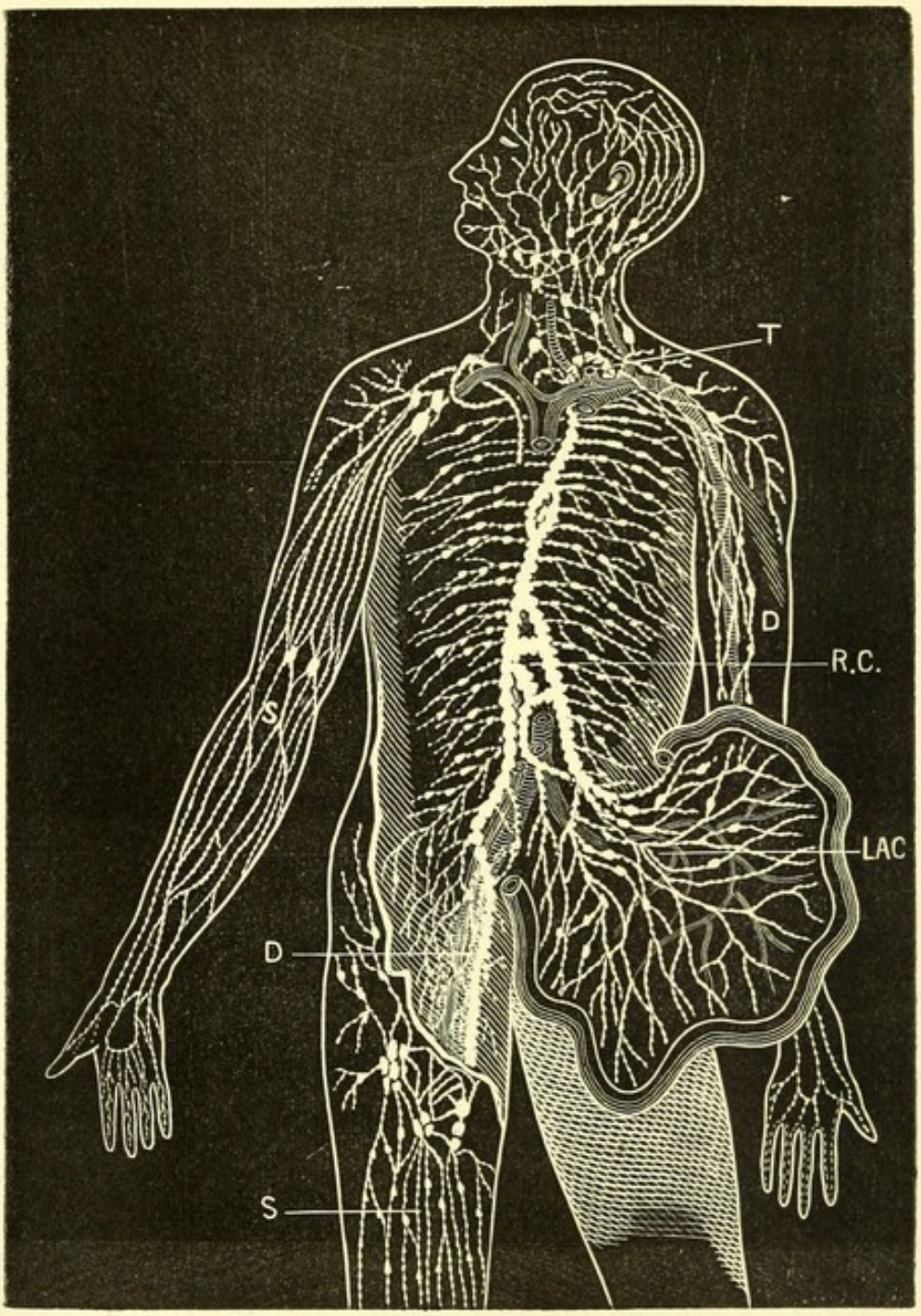


Fig. 80.—Diagram showing the Course of the Main Trunks of the Absorbent System. The lymphatics of lower extremities (D) meet the lacteals of intestines (LAC) at the receptaculum chyli (R. C.), where the thoracic duct begins. The superficial vessels are shown in the diagram on the right arm and leg (S), and the deeper ones on the arm to the left (D). The glands are here and there shown in groups. The small right duct opens into the veins on the right side. The thoracic duct opens into the union of the great veins of the left side of the neck (T).

system generally ; it may be well, therefore, at this place to give a brief account of the construction of the special apparatus which

carries on this function. Although the absorbent vessels form one continuous system, they may be conveniently divided into two departments, namely, interstitial and surface absorption. A certain modification of the latter, called the lacteal system, occurs in the alimentary canal, and is described under intestinal absorption.

I. *Interstitial Absorption.*

The blood flowing through the body in the delicate capillary vessels yields to the various tissues a kind of irrigation stream of plasma, which leaving the capillaries permeates every tissue and saturates them with nutrient fluid. The surplus of this irrigation stream is collected and carried back to the blood current by a special set of fine flattened vessels with slender walls, called the *lymph vascular system*, which acts as the drainage of the tissues, and pours its contents into the veins.

When the nutrient fluid escapes from the capillaries, it lies in the

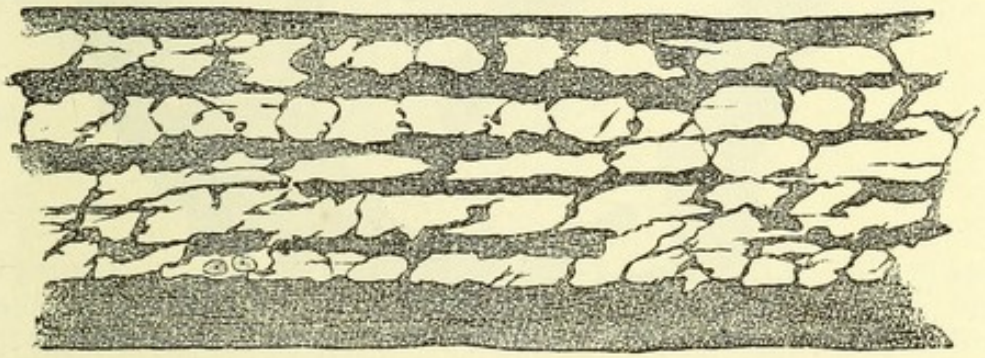


Fig. 81.—Tendon of Mouse's Tail treated with nitrate of silver, showing clefts or cell-spaces around the bundles of fibrils as white patches. These interstices may be called the smallest lymph-channels or spaces. (Schäfer.)

interstices between the tissue elements, and here bathes the cells which commonly occupy these *lymph spaces.* (Figs. 81 and 86.)

Communicating freely with the interstices of the tissues are irregular anastomosing flattened channels, which convey the lymph or any fluid forced between the tissues into vessels with definite boundaries. These vessels, which are lined with characteristic endothelium, form a more or less dense network of lymphatic capillaries, from which spring the tributaries of the lymph vessels. (Figs. 82 and 83.)

The lymphatic vessels are throughout slender thin-walled channels with frequent anastomoses and close-set valves, usually in pairs. They lie embedded in the connective tissue, and when empty are

difficult to see, owing to the extreme thinness of their coats. They converge towards a central vessel called the thoracic duct, which, passing from the abdominal cavity, through the thorax, reaches the left side of the neck, and opens into the angle of junction of the two great veins from the head and upper extremity. (Fig. 80.) On the

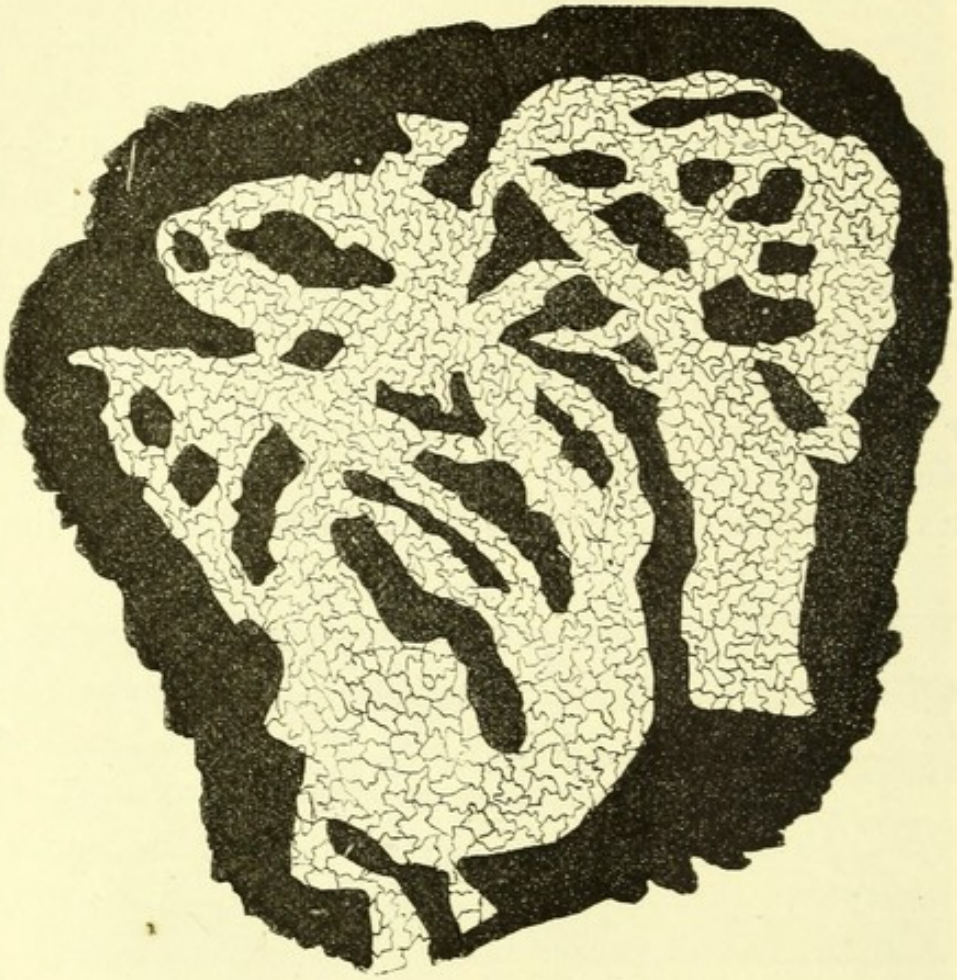


Fig. 82.—Lymph Channels from the thoracic side of the central tendon of the diaphragm of the rabbit, treated with silver nitrate. The fine lines indicate the boundaries of the endothelium cells lining the lymph channels. The dark part shows the islets between the lymphatic network. (Klein.)

right side a smaller trunk conveying the lymph from the right arm and that side of the head, chest, and neck, opens into the corresponding venous trunks.

The thoracic duct is much larger than any of the numerous tributaries which enter it at close intervals from all directions.

Its lower extremity or point of origin is an irregular dilatation called the *receptaculum chyli*, because the lymphatic vessels from the stomach and intestines, or *lacteals* as they are called, pour their contents into it. The chyle from the intestines thus flows into the same main channel as the lymph which is derived from the drainage of the tissues and organs of the lower extremity, the trunk and left side

of the head, neck and arm, and the two fluids are mixed in the receptaculum chyli, and other parts of the thoracic duct.

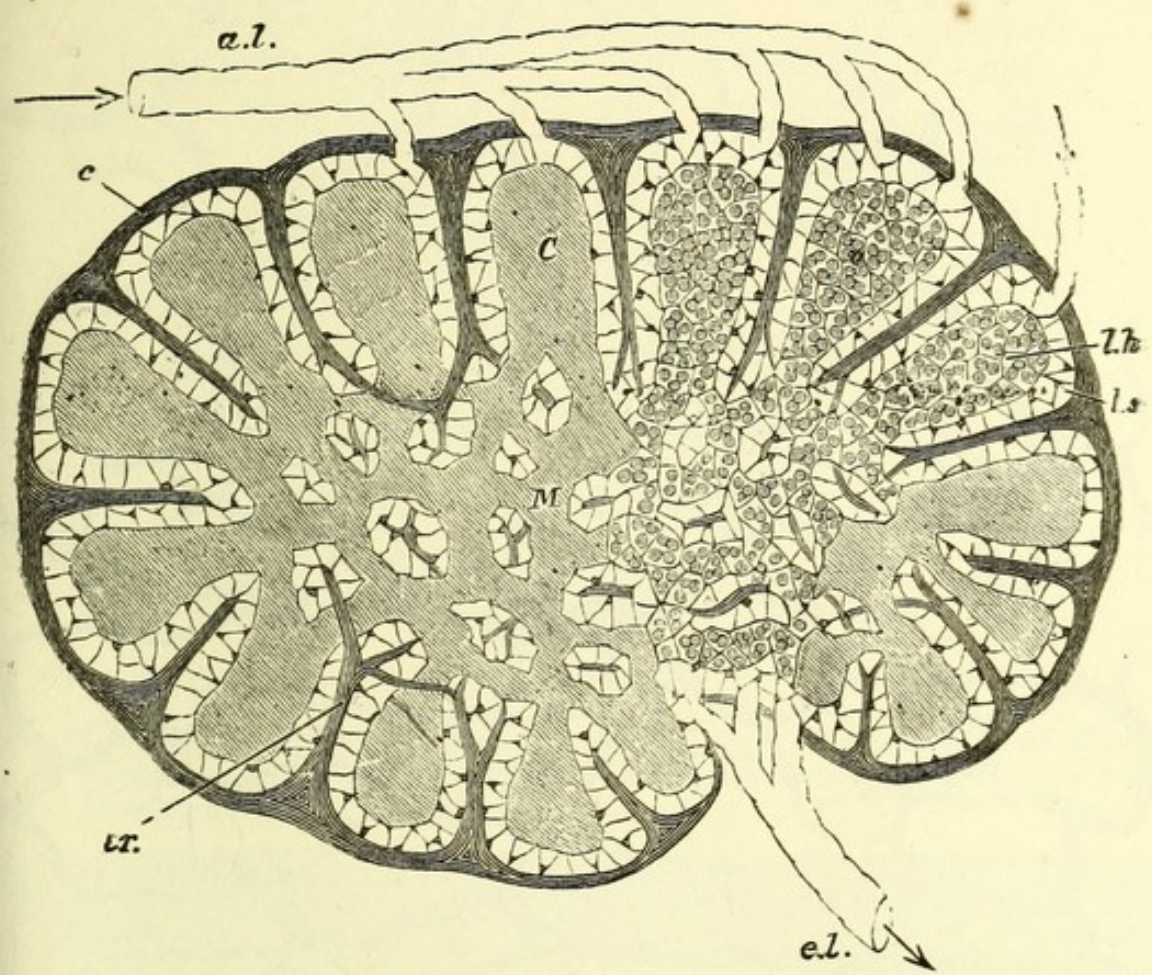


Fig. 83.—Diagram of a Lymphatic Gland, showing (*a l*) afferent and (*e l*) efferent lymphatic vessels; (C) Cortical substance; (M) Medullary substance; (*c*) Fibrous coat sending trabeculæ (*t r*) into the substance of the gland, where they branch, and in the medullary part form a reticulum, the trabeculæ are surrounded by the lymph path or sinus (*l s*), which separates them from the adenoid tissue (*l h*). (Sharpey.)

Lymphatic Glands, &c.

Along the course of the lymphatic vessels numerous small bodies called *lymphatic glands* or *follicles* are found, which are composed of a delicate trellis-work of adenoid tissue, packed with nucleated protoplasmic cells, called lymph corpuscles, the combination making what is known as *lymphoid tissue.* (Fig. 83 (*l h*) and 85 (*a*).) These masses of cells and their delicate supporting reticulum are enclosed in a fibrous case or capsule from which branching trabeculæ pass into the gland and separate the portions of lymphoid tissue from one another. The lymph channels enter and pour their contents through the convex side of the capsule. The lymph then flows through irregular paths, which lie between the lymph follicles next

to the capsule and trabeculæ, and lead to the concavity of the gland from which the efferent vessel escapes.

These lymph glands occur in groups in the flexures of the limbs

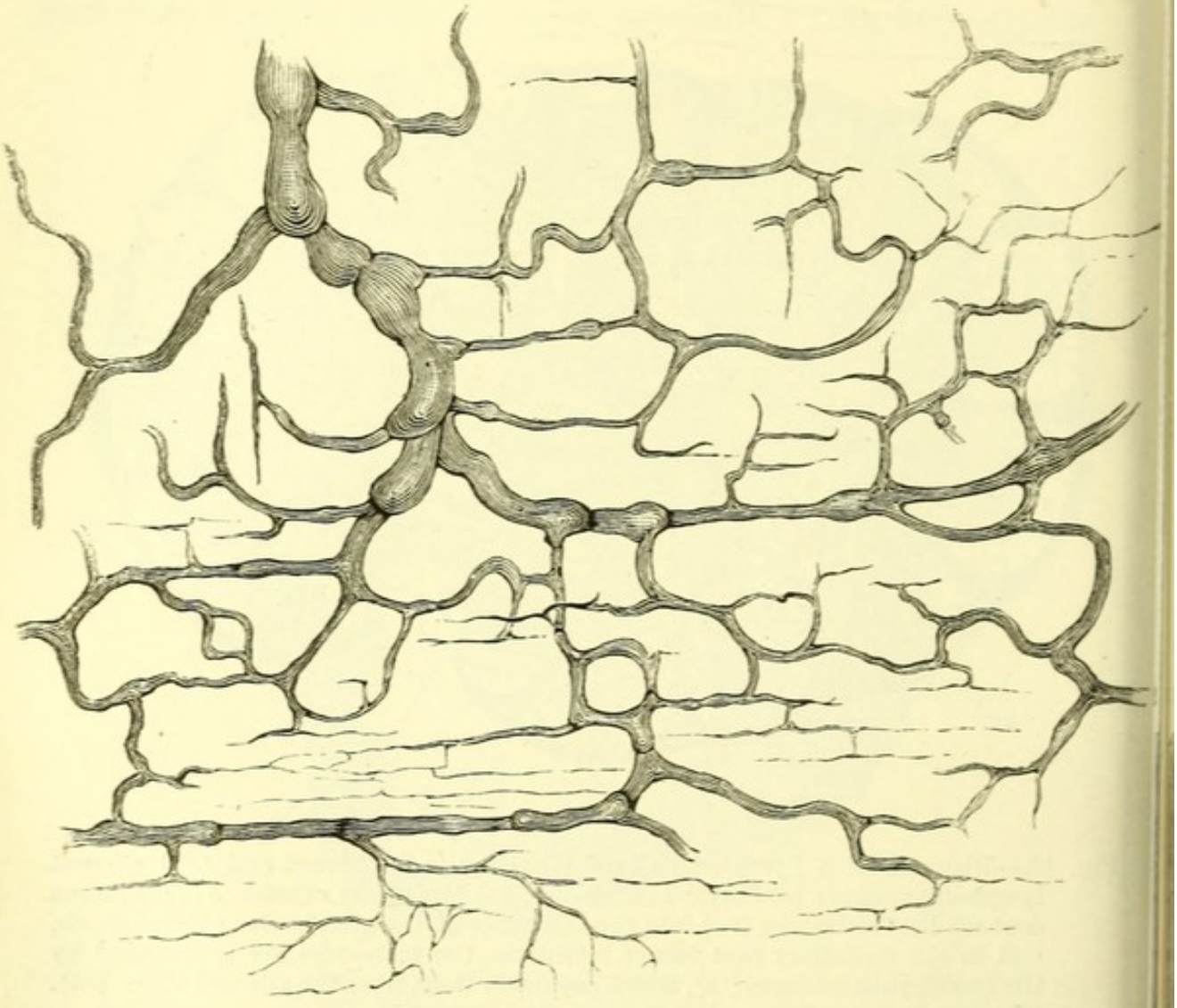


Fig. 84.—Lymphatic Network from between the Muscle Coats of the Intestinal Wall, with fine vessels and many valves, causing the walls to bulge. (Cadiat.)

the recesses of the neck, and the thoracic and abdominal cavities, a large number being placed in the mesentery, in the course of the intestinal lacteals.

In the submucous tissue of the intestine this lymphoid tissue is widely diffused, and here and there arranged in small follicles, which doubtless have a function similar to that of the lymph-glands found elsewhere.

Lymphatic Vessels.

There are various modes of origin of the lymphatic vessels which are more or less characteristic of the different parts in which they occur.

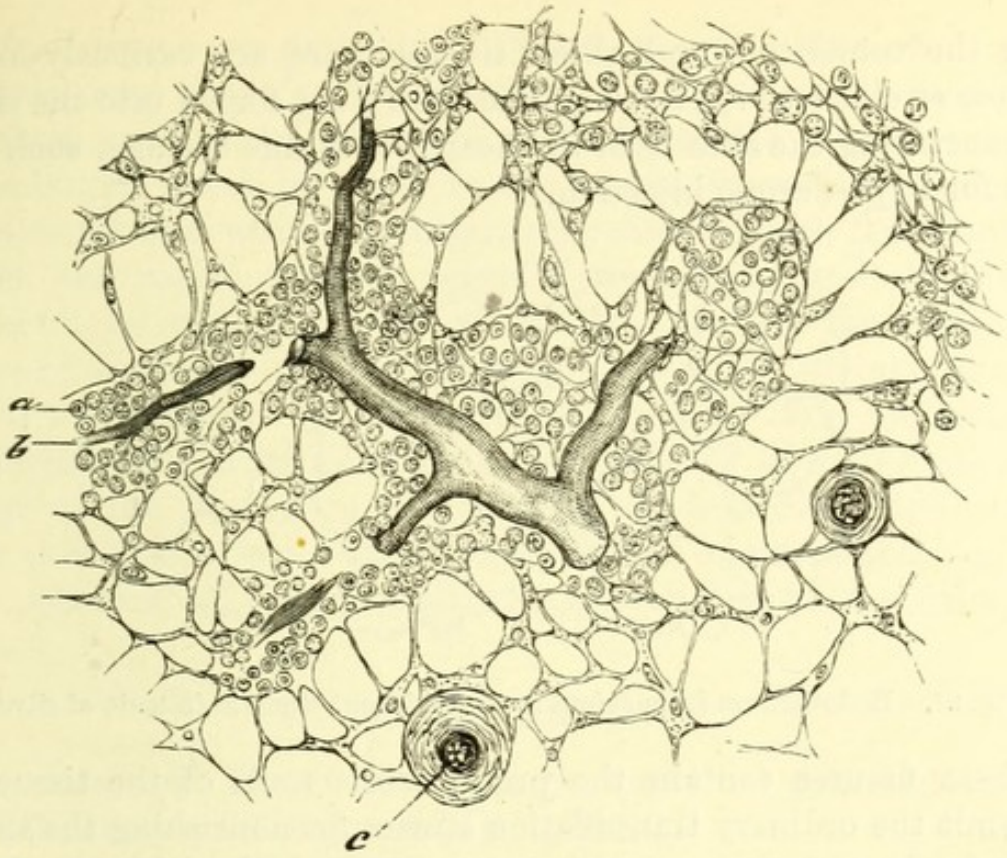


Fig. 85.—Section through the central or medullary part of a Lymphatic Gland, showing adenoid tissue (*a*) containing capillaries (*b*) and a fibrous trabecula (*c*) cut across showing a central artery. (Cadiat.)

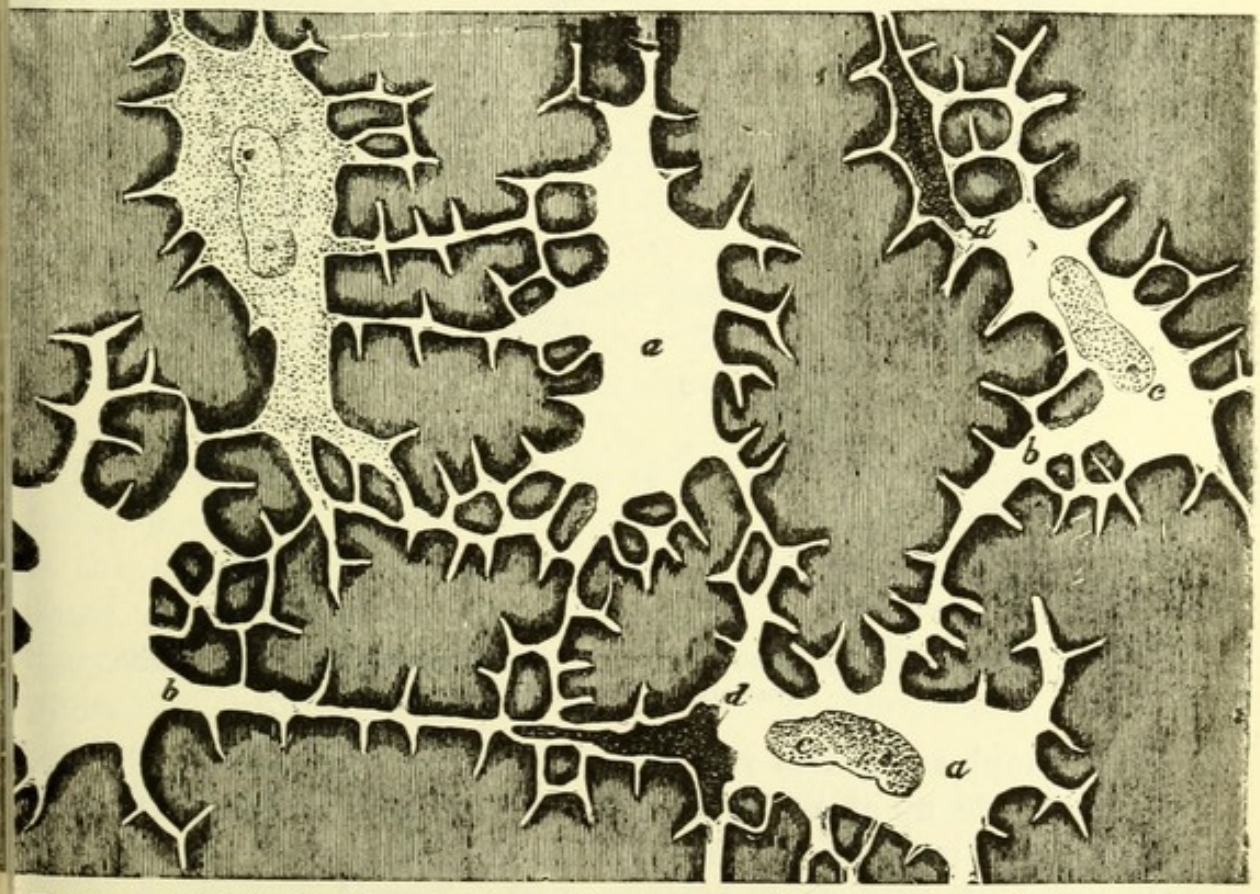


Fig. 86.—Clefts in the Corneal Tissue of a Frog treated with nitrate of silver, which leaves the spaces clear and stains the intermediate structure. These clefts (*a*) and their processes (*b*) form the lymph canalicular system, and at the same time are the spaces in which the corneal corpuscles reside. (Klein.)

In the connective and allied tissues there are variously-formed fissures or clefts which can be filled with fluid forced into the tissues by puncturing the skin with the nozzle of a fine syringe, such as is used for hypo-dermic injection.

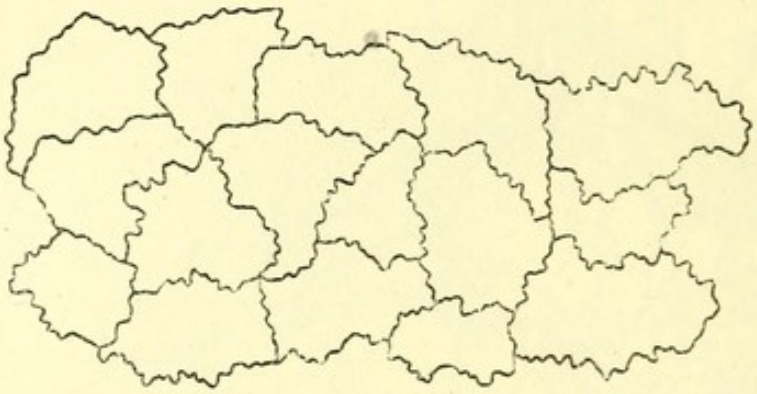


Fig. 87.—Endothelium from serous surface without stomata (nitrate of silver).

These fissures contain the protoplasmic units of the tissue, and transmit the ordinary transudation stream for nourishing the tissues. They freely communicate with one another, and lead into the beginnings of the network of lymphatic capillaries.

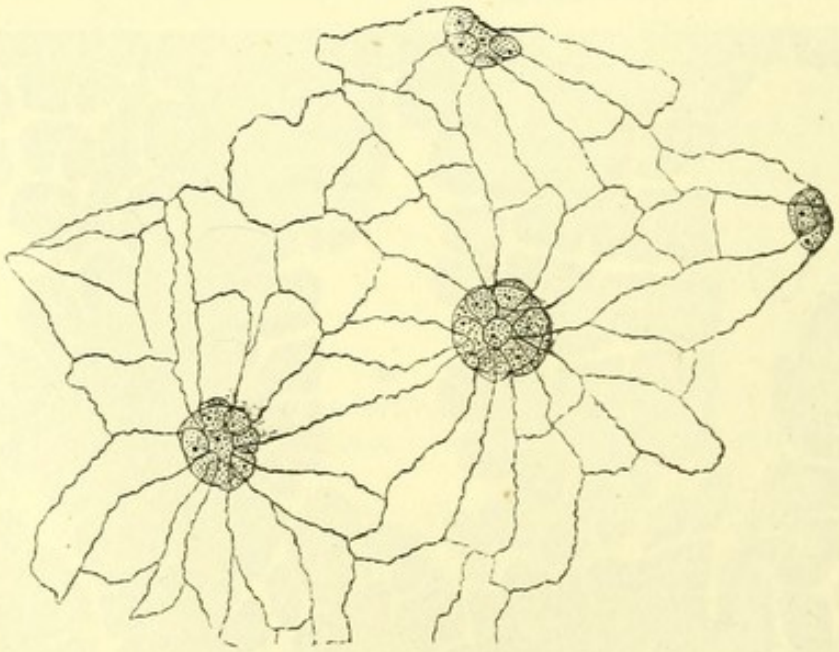


Fig. 88.—Endothelium from serous surface with stomata surrounded with granular protoplasmic cells.

The lymph capillaries run midway between the blood capillaries, and are made up of a single layer of nucleated endothelial cells, which can be brought to light with silver staining.

In some tissues, such as that of the central nervous system, liver and bone, the lymph vessels commence as channels encircling

the blood-vessels, or perivascular lymph spaces. Here the lymph channels form a kind of sheath for the minute blood-vessels, and pass along to the connective tissue of the adventitia of the larger.

The lymph vessels may also be said to commence on the surface of serous membranes which are intimately connected with the lymphatic system, and may indeed be regarded as nothing more than inordinately developed lymph spaces. In most parts of the endothelial surface of serous cavities are a number of so-called *stomata*, or small apertures surrounded by a few cells, which differ from the ordinary endothelial cells in many respects, and probably have to control the passage of the fluid from the serous cavity into the lymph vessels. These stomata are found to be placed at the commencement of the dense network of lymph capillaries, which lies in the subserous tissue.

II. *Intestinal Absorption.*

The intestinal absorbents form a special department of the lymphatic system aiding nutrition. On account of the white chyle seen as a milky fluid through their transparent walls, they have been called *lacteals*. Their functions are to take up the nutrient fluid from the intestinal cavity, and to drain the tissue in which they lie. In order to fulfil these functions, they are arranged in a particular way, especially adapted to the peculiar construction of the mucous membrane lining this part of the alimentary tract, which must be briefly described before the mechanism of absorption can be understood.

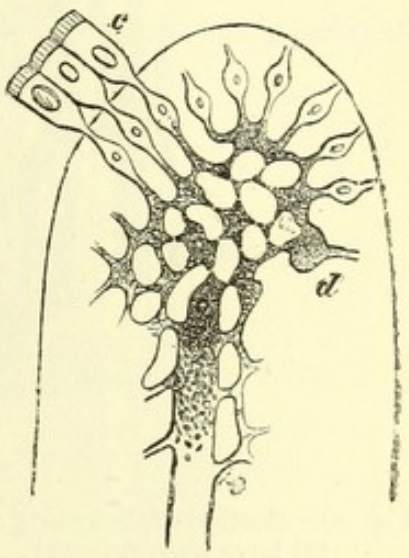


Fig. 89.—Diagram of relation of the epithelium to the lacteal radical in villus. The protoplasmic epithelial cells supposed to be connected to the absorbent vessel by adenoid tissue. (After Funke.)

The most striking characteristic of the lining membrane of the small intestine is the existence of *villi*, which are only found in this part of the alimentary tract. They consist of nipple-shaped processes, projecting into the intestinal cavity, so closely set that they have the appearance of the pile of velvet; and being just visible to the naked eye, they give the mucous membrane, when washed and held under water, a peculiar velvety look. By means of these villi, and also of the ring-like folds of mucous membrane in the upper part of the

small intestine, the extent of surface over which the chyme has to travel is greatly increased.

The surface of the villi is covered over with a simple layer of columnar epithelial cells in continuity with the epithelium lining

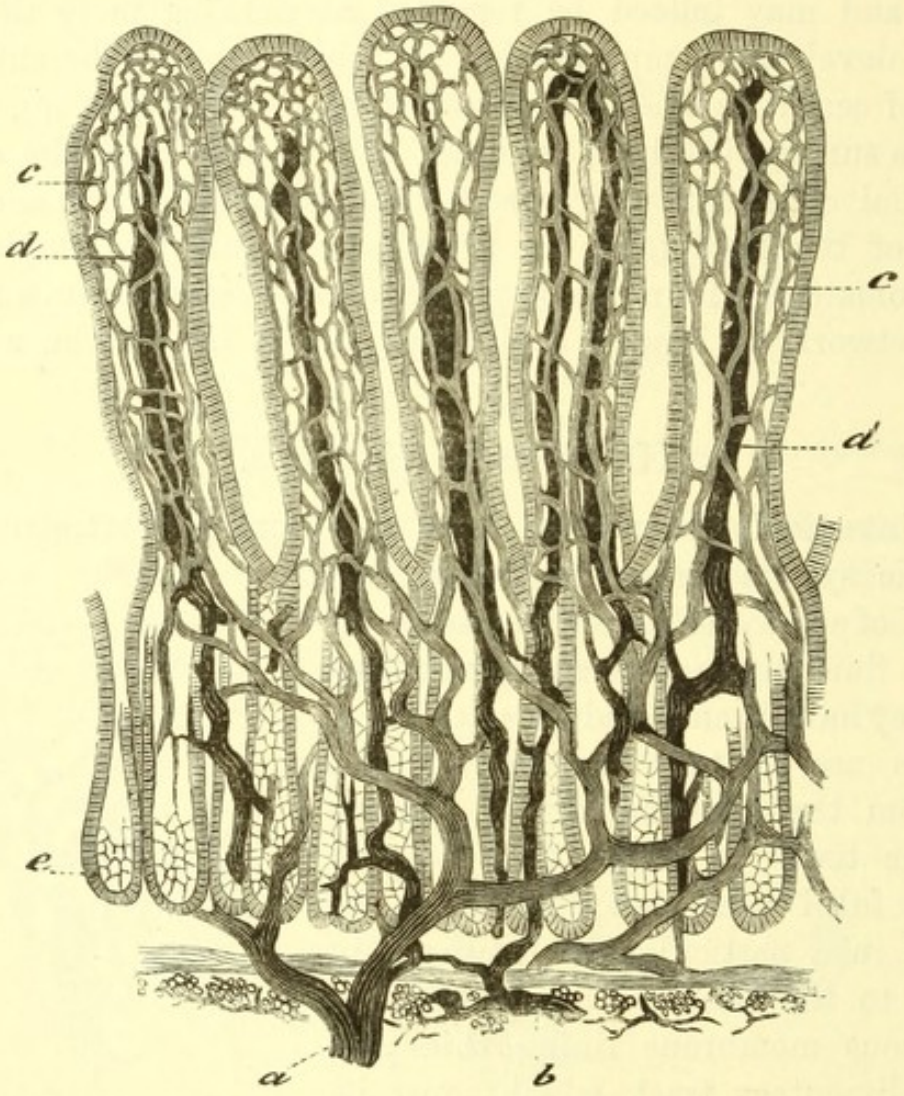


Fig. 90.—Section of Intestine of a Dog in which the blood-vessels (*c*) and the lacteals (*d*) have been injected. The blind ending or simple loop of the black lacteal is seen to be surrounded by the capillary network of the blood-vessels. (Cadiat.)

the rest of the intestinal tract. The free surface of these cells is marked by a clear striated margin composed of a row of minute rods closely packed together, while the deep-seated end of the cells is branched, and appears to be prolonged into the substance of the villus and in some way to be connected with the supporting retiform tissue. Some of the cells are seen to swell upon the addition of certain re-agents, owing to their containing mucus, which gives them a peculiar goblet shape; hence they are called goblet cells. These occur at intervals, and some observers consider that they form a distinct variety, differing from the neighbouring cells

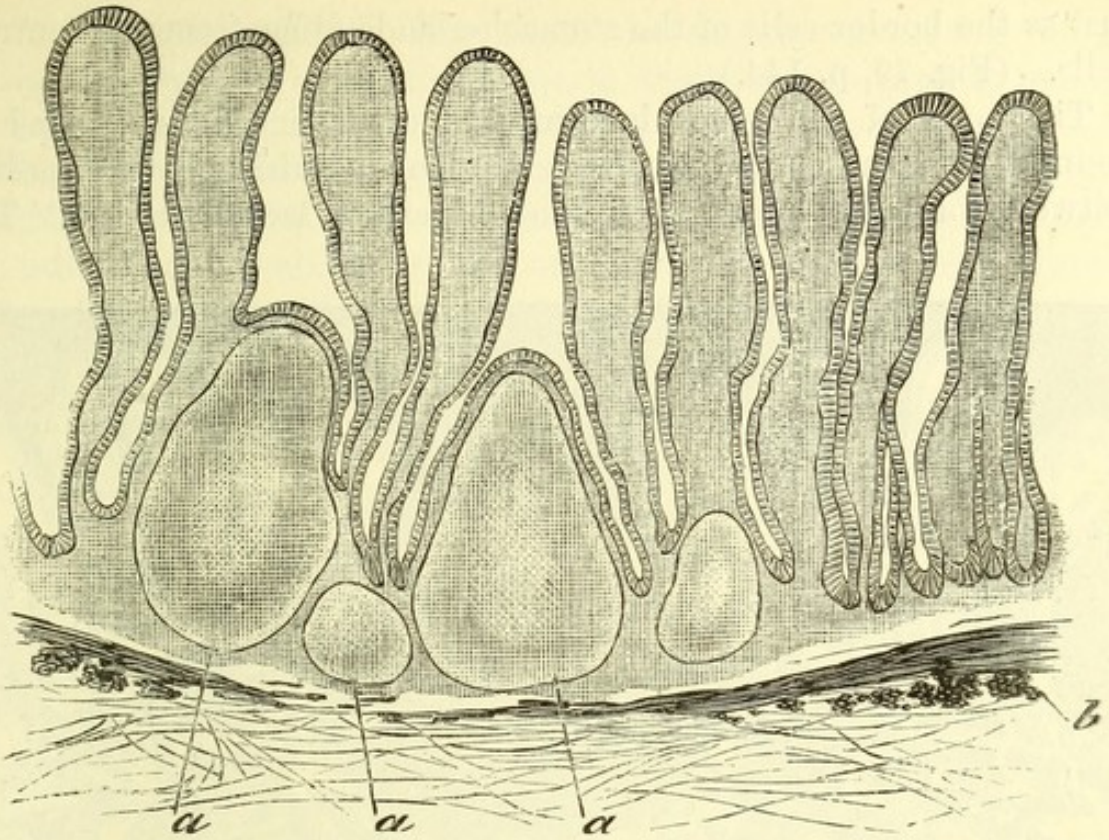


Fig. 91.—Diagram of Section of the Mucous Membrane of the Intestine, showing the position of the lymph follicles (*a*). (Cadiat.)

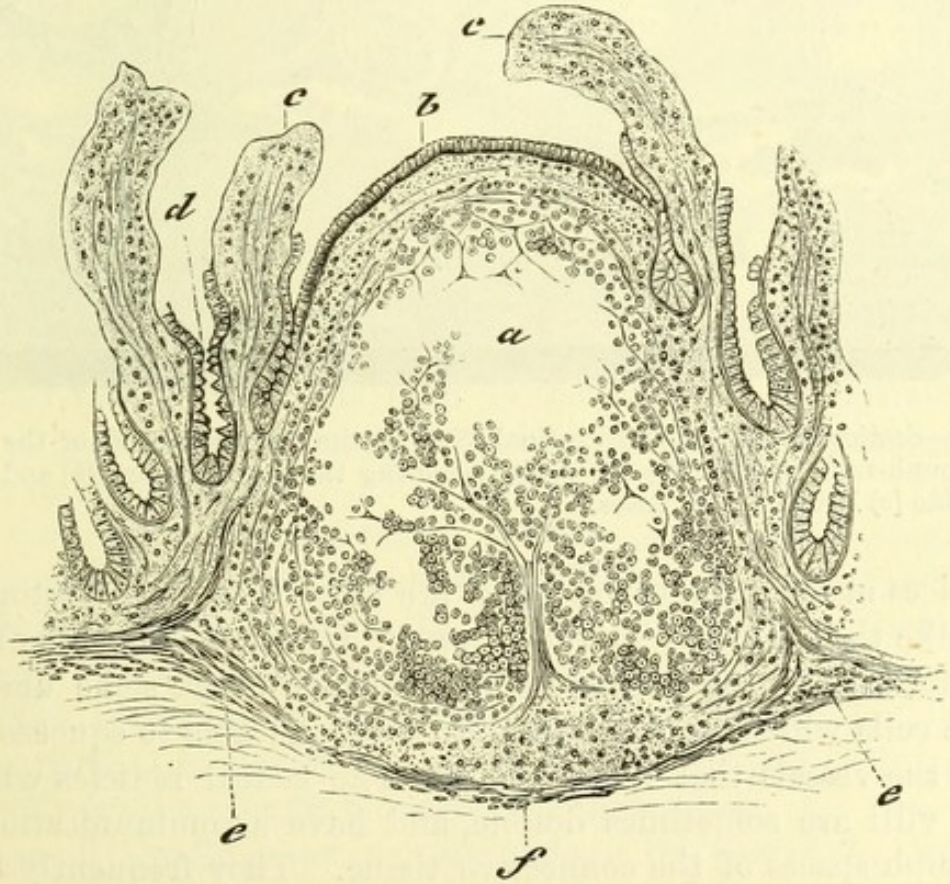


Fig. 92.—Section of Single Lymph-follicle of the Small Intestine, showing (*a*) follicle covered with epithelium (*b*), which has fallen from the villi (*c*); (*d*) Lieberkühn's follicles; (*e*) Muscularis mucosæ. (Cadiat.)

just as the border-cells of the stomach-glands differ from the central-cells. (Fig. 79, p. 144.)

The body of the villus is composed of a very delicate kind of connective tissue, forming a slender frame in which a little cage-like network of blood-vessels surrounds a central lacteal radicle. The

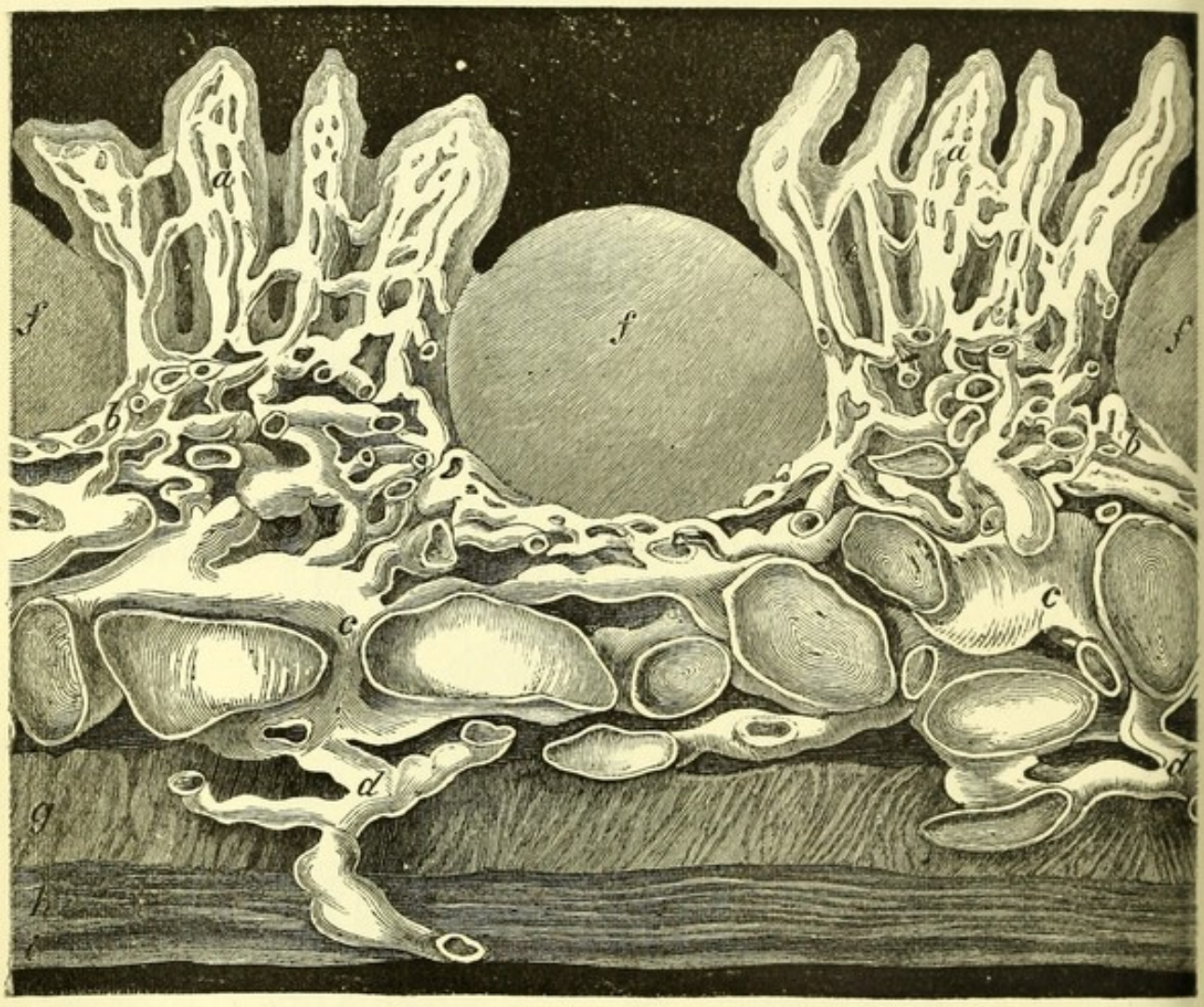


Fig. 93.—Section through the Intestinal Wall in the neighbourhood of the grouped lymph-follicles (*f*) (Peyer's patch), showing the upper narrow (*b*) and the deep wide (*c*) lymphatic plexuses.

interstices of this connective tissue are filled with pale protoplasmic cells, like those formed in the lymph. Under the basement membrane forming the foundation of the epithelium are some unstriated muscle cells which embrace the villus and are able to squeeze it and empty the vessels that lie within it. The lacteal radicles which lie in the villi are sometimes double, and have a communication with the lymph spaces of the connective tissue. They frequently branch as they pass down from the villi to reach the dense network of lacteal vessels which lies beneath the mucous membrane. (Fig. 93.)

At irregular intervals throughout the submucous tissue are found masses of lymphoid tissue similar to those seen in packets within a lymph gland or in other lymph follicles. These are either isolated (solitary glands) or collected into groups (agminated glands or Peyer's patches). Though called glands by anatomists, it should be borne in mind that they are in no way connected with the secretion of any of the intestinal juices, but belong to the absorbing arrangements of the intestine. Around these solitary and grouped lymph follicles are spaces and networks from which the lacteal vsesels arise (fig. 93).

Mechanism of Absorption.

Formerly absorption was supposed to take place by means of the blood-vessels alone. After the discovery of lymph and chyle vessels by Caspar Aselli the belief in the direct absorption by the blood-vessels was abandoned, and all the work of absorption was attributed to the lymphatics. Now, however, ample evidence exists to show that substances capable of absorption can make their way into the blood-vessels of any part not protected by an impermeable covering like the horny layer of the skin, and thus be carried directly to the general circulation. The share taken by the blood-vessels in interstitial absorption in the tissues is not defined, and when no impediment to the lymph-flow exists is probably insignificant.

In the absorption from the alimentary tract the blood-vessels appear to take a considerable part.

How far the tissue interspaces and the local lymph-channels, many of which surround the blood-vessels, aid in the passage of substances into the blood-currents is not known; but they probably have some such effect, for the experiments showing direct absorption by the blood-vessels leave the local lymph-channels in operation and at the same time the normal flow of lymph towards the thoracic duct is more or less hindered.

We can easily imagine that a surface covered by a single layer of epithelial cells, with numerous blood-vessels and a good supply of absorbents beneath them, is capable of absorbing materials in solution ; and we know that large quantities of fluids and solutions of various materials are absorbed from the stomach and large intestine, partly, no doubt, by means of the lacteals or lymphatics, and partly by the minute blood-vessels themselves.

The small intestine, however, seems to be the part of the alimentary tract which is especially adapted for taking up the materials elaborated from the food.

In the upper part of the small intestine the valvulæ conniventes are most marked, and the villi are long and set closely together. It is here we find the thickest layer of creamy chyme covering the mucous membrane, but seldom any masses of undigested food. All these points tend to show that the upper part of the small intestine is the part specially adapted for absorption. The chyme which clings to the mucous membrane contains all the substances destined to pass into the economy. Into this mixture the villi dip, so that each villus is bathed in chyme. From what has been said of the construction of the villi it is obvious that such an arrangement is well adapted to the absorption of the nutrient material, which is in the closest proximity to the lacteals and blood-vessels.

The various foodstuffs in the chyme differ in the degree of readiness with which they are absorbed. Hence the facility of absorption of its principal ingredients must be examined separately in detail.

Water can be absorbed from the intestinal tract in almost unlimited quantity, but not solutions of salts. The amount of the solution of any salt capable of absorption seems to depend on its endosmotic equivalent. The lower the endosmotic equivalent the more readily the solution passes into the blood-vessels. In those cases where the equivalent is very high, such as magnesium sulphate, there is a tendency of the fluid to pass out from the blood-vessels into the intestinal cavity; this has been supposed to explain the watery stools caused by this and such-like saline purgatives.

Among the carbo-hydrates we need only take into account the sugars, for starch unchanged is but little if at all absorbed. Only a certain quantity of sugar can be taken up by the intestinal absorbents, since some is found in the fæces when the amount taken with the food exceeds a certain quantity. Some of the sugar in the intestine undergoes fermentation, by which it is converted into lactic and butyric acid. The quantity of sugar absorbed as lactic and butyric acid has not been determined, but the amount found in the portal vessels or lacteals does not appear to correspond with that which disappears from the cavity of the intestine.

Ordinary proteids, being colloids, can only pass with difficulty through an animal membrane, hence it is supposed that they must be changed during digestion into peptones before they can be absorbed. Their absorption takes place readily in the stomach, and is completed in the small intestine, as only a small quantity of albuminous substances is found in the large intestine even after an

excessive meat diet. The more concentrated the solutions of peptones the more rapidly are they absorbed, and the rate of absorption is greatest at first and then by degrees diminishes. The presence of free alkali is said to facilitate the absorption of peptones. It is a curious fact that neither in the lacteals nor in the portal blood can any quantity of peptones be found, even during active proteid digestion; so that it is impossible to trace out their course as peptones, or to say by which set of absorbent channels they reach the blood. If we assume that all proteids must be absorbed as diffusible peptones, we are forced to conclude that during their passage from the intestinal cavity they must be reconverted into ordinary proteids. But we know that soluble forms of albumin are to some extent diffusible (when a solution of salt is used) through a dead animal membrane. But even were they quite indiffusible this fact would not preclude the possibility of their passing through the intestinal wall, which is a living structure not restricted by such physical difficulties as are met with in diffusion through an inanimate membrane. When we know that solid particles of fat can enter the lacteals (an event which we cannot explain physically), we can have no difficulty in believing that an insoluble solution of albumin may also be admitted. We may then conclude that it is not only possible, but even probable, that a good deal of proteid is absorbed as ordinary soluble albumin. A certain limit to proteid absorption exists, so that if an amount of albuminous material above the maximum that can be absorbed be eaten, the albumins are either converted into leucin and tyrosin, or thrown off with the fæces.

In the absorption of water, watery solutions of salts, sugars, and peptones by the lacteals, there are no great physical difficulties to be got over; so that we are in the habit of speaking confidently about the mechanism of their absorption, although in all probability many circumstances connected with the life of the epithelial cells, &c., of which we are ignorant, co-operate in bringing about the results which seem to us so simple to explain in our own fashion.

It is not so with the fatty food-stuffs. A small quantity of these may, no doubt, be split up into soluble glycerine and fatty acids, which are at once changed into soluble soaps, and in this condition are capable of simple osmotic transmission into the blood-vessels or lacteals. The greater portion of fat enters the lacteals as fat in the condition of fine emulsion, *i.e.*, composed of solid particles. This process is difficult to reconcile with our physical experiences; for, however finely divided it may be, fat emulsified

does not pass through an animal membrane more freely than ordinary fluid fat.

The fat emulsion is chiefly taken up by the villi of the small intestines, for in the stomach it exists only in large fluid masses or globules, and the amount of fat found in the large intestine is small, unless used as food in great excess. This can also be seen in examining the absorbent vessels after a fatty meal, when those, which carry materials from the stomach and large intestine are clear and transparent, while those coming from the small intestines are filled with the white milky fluid which gives them their special name of lacteals. There is a limit to the absorbent capacity of the intestine for fatty matters, for when a great excess of fat is eaten it appears with the excrement, sometimes giving rise to adipose diarrhœa, thus showing that the amount has exceeded this limit.

The important question remains, how does the fat emulsion make its way through the intestinal mucous membrane? That it really does so there can be no shadow of doubt; for it disappears from the intestinal cavity, and can be detected in the chyle with the aid of the microscope more easily than any other of the intestinal contents absorbed.

It has been shown that while a membrane moistened with water acts as a complete barrier to a fat emulsion, and only after prolonged exposure under high pressure allows traces of fat to pass, the same membrane when saturated with bile will without pressure permit the passage of a considerable amount of oil. It has, therefore, been suggested that the epithelial cells of the mucous membrane are more or less moistened with bile, and the particles of fat in the emulsion are also coated, as it were, with a film of bile or soap. Thus they are enabled to pass into the epithelial cells, in which they can be detected during digestion. The bile or soapy coating of the fat particles may, no doubt, aid in their transit through the various obstacles met on their way to the lacteal radicles, but the course taken by the fat particles can hardly be explained in this way. Many circumstances force us to believe that the activity of the protoplasm of the epithelial or some special wandering cells forms a necessary factor in the case.

By means of osmic acid, which renders the fat granules black, they may be demonstrated to occur in the following situations during the active digestion of fat. 1. In many of the epithelial cells lining the villi &c. 2. In lymph-cells lying in close relation to the epithelium and others in the lymphoid tissue of the villi. 3. Between the epithelial cells; possibly held here by processes from

the amœboid lymph-cells. The fat particles are then either taken up by the epithelial cells from the cavity of the intestine, and handed over to the subjacent lymph-cells, or seized by the protoplasmic processes of the lymph-cells which pass between the epithelial cells to reach the surface.

When the fat is once lodged in the protoplasm of the cells these amœboid elements convey it through the delicate connective tissue of the villi to the lacteal radicle. Other forces, such as the contraction of the villi, may aid in their further movement to the central lacteal space of the villus.

The exact utility of the marginal bands of rods or pores which characterize the surface of the intestinal epithelium is not known, though it has been supposed to be connected with the absorption of fats.

We may conclude, then, that the passage through the intestinal wall of some of the materials taken as food may possibly be accomplished by mere physical processes, but it is probable that the vital activity of the epithelial cells controls the absorption of all food-stuffs. The passage of the fat can only be explained by the aid of the direct activity of cells which by amœboid movement take up the fine particles and pass them on to the interstices of the connective tissue of the villi.

Lymph and Chyle.

As these two fluids are generally mixed in the thoracic duct, whence the lymph is commonly obtained for examination, we may discuss them together, though the lymph might more properly be considered with the distribution of the nutrient materials to the tissues.

The fluids coming from the tissue-drainage, from the lymphatic glands and from the lacteals of the alimentary tract, when mingled in the thoracic duct, form an opaque mixture which holds a considerable quantity of proteid in solution, and contains a number of morphological elements, viz. : (1), protoplasmic cells similar to those found in the lymph follicles, and in most essential points identical with the pale cells found in the blood ; (2), some red-blood corpuscles which give the fluid in the thoracic duct a pinkish colour ; (3), a quantity of very finely divided fat, which varies in proportion to the amount of fat recently digested ; (4), other minute particles of unknown function and origin.

When removed from the body and allowed to stand, the lymph

becomes converted into a soft jelly. This coagulation, no doubt, depends upon the chemical changes in the lymph which give rise to fibrin, the formation of which will be discussed more fully in a future chapter. The amount of fibrin formed in the lymph is very small, and, therefore, the clot is very soft, and shrinks considerably.

The lymph of the thoracic duct contains three forms of proteid: (1), serum albumin, which can be coagulated by heat; (2), alkali albumin precipitated by neutralization; and (3), globulin. It also contains soap in solution, cholesterin, grape-sugar, urea, leucin, and some salts, particularly sodium chloride, and the sulphates and phosphates of the alkalies.

The quantity of *chyle* which can be obtained from the lacteals is small, and, therefore, its thorough investigation is difficult. The fluid from the lacteals differs from the mixed lymph in appearance and constitution only during digestion, and then chiefly in containing a greater amount of fat and solids derived from the intestinal cavity.

On their way to enter into the blood-current both the lymph and chyle undergo changes. Before passing through the lymphatic glands the fluid contains much fewer lymph corpuscles than after it has traversed the glands: from this fact and from the structure of the lymph glands we may conclude that they are the chief sources of these white cells. The chyle of the lacteal vessel of the mesentery contains particles of fat which greatly exceed in size those found in the thoracic duct, so we may infer that the fat emulsion undergoes a further subdivision or modification on its way through the glands.

Lymph which has been collected from the lymph channels of the extremities is an almost clear colourless fluid, rich in the waste products of tissue change, but containing less albumin than that coming from the main trunk, and no fat. After long fasting the lymph from the thoracic duct has the same characters.

Lymph contains a considerable quantity of carbonic acid gas, about 50 vol. per cent., some of which is readily removed by the air-pump, and is therefore said to be absorbed by the fluid, while some can only be removed by the addition of acids, and therefore is considered to be in chemical combination. Only mere traces of oxygen have been found in the lymph.

The quantity of chyle and lymph poured into the blood varies so much that any estimation of the amount entering in a given time is unreliable.

The following circumstances upon which the variations may depend are instructive :—

1. The ingestion of liquid and solid food causes a great increase in the amount of chyle. This is obvious from the change in the state of the lacteal vessels, which, from being transparent and almost empty, become widely distended and white.
2. The activity of any organ causes an increase of lymph to flow from it.
3. Impediment to the return of the venous blood from any part increases the irrigation, and hence the lymph.
4. Increase of the amount or the pressure of the blood flowing through any part augments the lymph flow.
5. The administration of curare increases the amount of lymph.

The history of the structural elements or lymph-corpuscles, which exist in such numbers in the large lymph-channels, requires some further discussion, as these cells are composed of active protoplasm destined for some important function, and must be produced by some vital process.

The origin of the lymph corpuscle is not restricted to any one part of the body or to any special organ. It has been already said that the lymphatic glands are the most important source of these cells, because the follicular tissue is filled with them, and the lymph contains a much larger number after it has passed through some lymph glands. In the lymphoid tissue of the spleen and the intestinal mucous membrane they are very numerous, and, no doubt, many have their origin in the follicular tissue of that organ and intestine. They are said also to be formed in the red marrow of the bones. Although their number is relatively small, lymphatic cells occur even in those lymph-channels that are unconnected with a lymphatic gland, and these cells, no doubt, come from the blood, which contains many cell-elements, identical with the lymph-cells found in the lymphatic duct. These cells, when they arrive at the minute blood-vessels sometimes leave the vessels and creep by amœboid movements into the interstices of the tissue with the irrigation stream. They may permanently abide in the tissue, or be washed back into the larger lymph-channels with the surplus stream of lymph. When the abnormal increase of activity in a tissue known as inflammation occurs, this escape of the white cells from the blood takes place with great rapidity, and the stages in the process can be watched under the microscope.

Still another source of the lymph-cells may be from proliferation of the cells which lie in the tissues. The fixed tissue-cells are said to be capable of producing elements identical with lymph-cells, which by division possibly multiply and produce their like, and may be carried along by the lymph-stream as lymph-cells.

The enormous number of cells which accumulate as pus when an abscess forms are structurally identical with lymph-cells, and probably arise from these combined sources, viz., escape from the blood-vessels and proliferation of the tissue-cells.

The lymph-cells, therefore, whether they have their origin in a lymph-gland, spleen, or connective tissue, perform a kind of circuit, going with the lymph into the blood, and are distributed with the latter to the tissues, whence they may be once more carried into the lymph-stream.

Movement of the Lymph.

In some of the lower animals small muscular sacs occur in the course of the main lymph-channels, which pump the lymph into the great veins by contracting rhythmically much in the same way as the heart.

In man and the higher animals no such *lymph-hearts* have been found; the onward movement of the fluid depends chiefly on the pressure under which the irrigation stream leaves the blood-vessels. The fluid in the blood-vessels, as we shall presently see, is under considerable pressure, which causes the plasma to leave the capillaries. Hence, if a lymphatic trunk be tied, its tributaries are filled with lymph until a considerable pressure (8—10 mm., soda solution) is developed in their radicles.

While the pressure exerted on the small tributaries of the lymph channel may become considerable, that in the thoracic duct is invariably very low for the following reasons. The blood in the large veins into which the duct opens is under less pressure than in any other part of the vascular system, owing to the thoracic suction, or negative pressure in the thorax, caused by the elastic traction of the lungs. In fact, the pressure in the large veins, *e.g.*, brachial, &c., varies from 0 to −4 mm. Hg., and that in the venæ cavæ is always negative, except in sudden or forced expiration, and varies, according to the period of the respiratory rhythm, from −5 mm., in inspiration, to −2 mm. in expiration.

The fact that the lymph at the origin of the small channels is at a pressure of 8 to 10 mm. of water, whilst at the entrance to the vein

it is nil, would be sufficient to explain the movement, even if there were no other force aiding it.

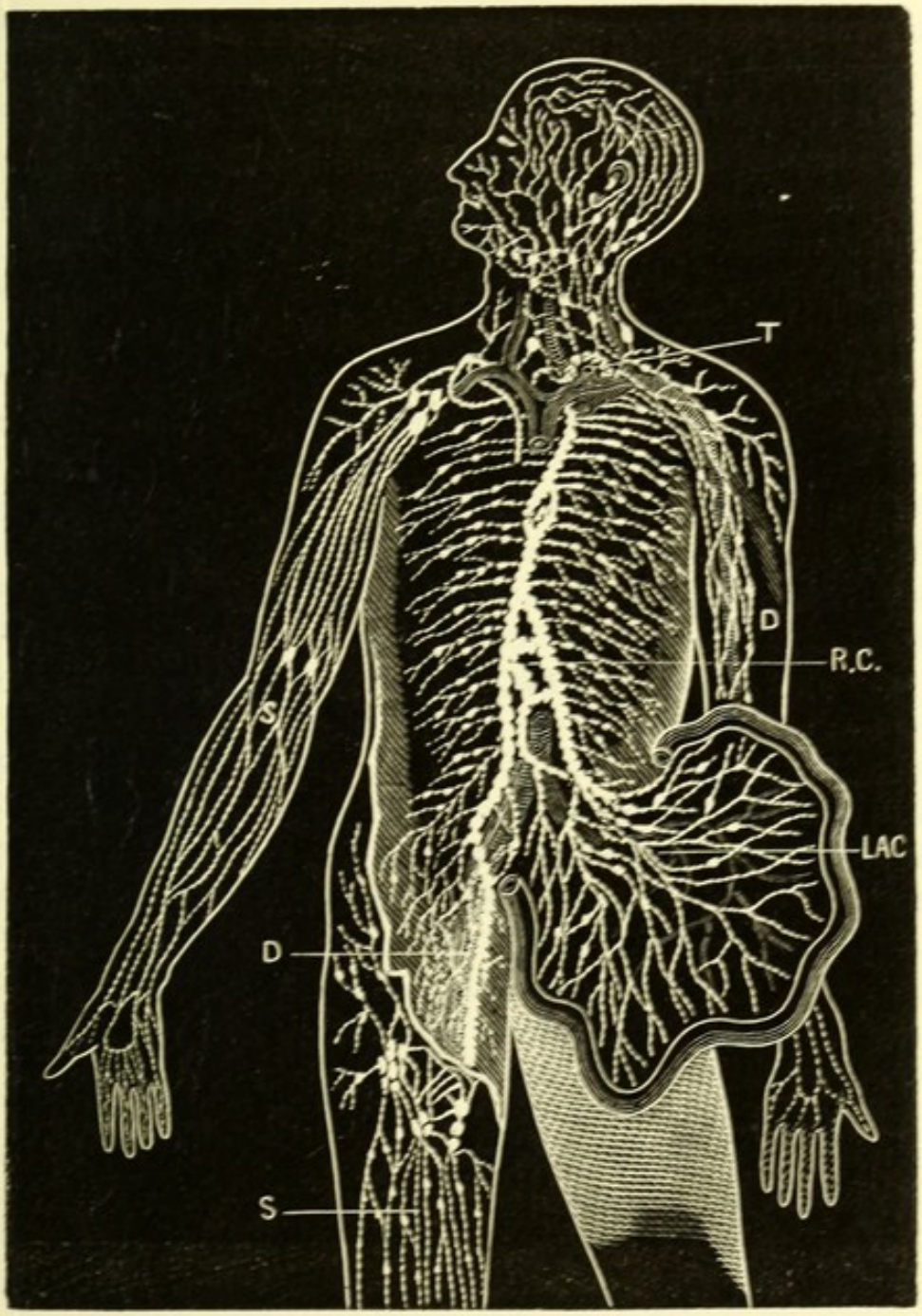


Fig. 94.—Diagram showing the Course of the Main Trunks of the Absorbent System. The lymphatics of lower extremities (D) meet the lacteals of intestines (LAC) at the receptaculum chyli (R. C.), where the thoracic duct begins. The superficial vessels are shown in the diagram on the right arm and leg (S), and the deeper ones on the arm to the left (D). The glands are here and there shown in groups. The small right duct opens into the veins on the right side. The thoracic duct opens into the union of the great veins of the left side of the neck (T).

It must be remembered that every lymph-vessel is furnished with closely set valves, which prevent the fluid it contains from being

forced backwards, so that any accidental local pressure exercised on the exterior of a lymph-channel helps the fluid onwards to the veins. Along their entire extent these vessels are subject to certain forces which must materially aid the flow of the lymph-stream. The first of these is the pressure exerted on the small vessels by the movement of the muscles in the neighbourhood. The second is the unequal distribution of atmospheric pressure, which has full force on the peripheral channels, but is kept off the thoracic duct and its termination, as already mentioned, by the rigidity of the thoracic wall, which, together with the tendency of the elastic lungs to shrink, causes a permanent negative pressure in the thoracic cavity through which the duct passes. And lastly, the thin-walled lymphatics are everywhere surrounded with very elastic textures enclosed in an elastic skin which exert an amount of pressure, sufficient to empty and press together the walls of the vessels after death, and therefore during life must have considerable influence upon the fluid they contain.

The movements of the chyle depend on the same forces, with the addition of the power used in the contraction of the villi, which pump the chyle from the lacteal radicles into the network of valved vessels in the submucous tissue.

The commencements of the thoracic duct and the lacteals are placed in the abdominal cavity, and therefore are constantly under the influence of the positive pressure exerted by the abdominal wall on the contained viscera. The rest of the duct is in the thorax, where the pressure is habitually negative. Certain variations coincident with inspiration and expiration take place in both these cavities, and must aid the onward flow of fluid in a vessel containing valves so closely set.

CHAPTER XIII.

THE CONSTITUTION OF THE BLOOD.

In all animals, except those which form the lowest class (Protozoa), the distribution of the nutritious materials to the various parts of the body, as well as the collection of the effete matters prior to their expulsion, is carried on by the medium of a fluid which circulates through the different parts of the body. This fluid is the blood.

In vertebrate animals the blood passes through a closed system of elastic pipes and is kept in constant motion by the action of a muscular pump. It is first forced through strong, branching canals called arteries, whose walls gradually become thinner as the branches get smaller, and end in a network of delicate channels (capillaries), through which it slowly trickles into the wide soft-walled veins by means of which it flows gently back again to the heart. In its course it receives the nutritive materials from the stomach and intestines after digestion, the specially elaborated substances from the liver, spleen, and lymph glands, and the oxygen absorbed from the air in the lungs. In short, it contains and bears to their destination all the materials required for the chemical changes of the economy. While passing through the capillary networks of the various tissues, it takes up the waste materials resulting from the tissue-changes and bears them to their proper point of exit from the body; at the same time the nutriment oozes through the delicate vessel walls and is diffused in the tissues.

General Characteristics of the Blood.

The blood of vertebrate animals is a bright scarlet colour when exposed to the oxygen of the air, but when not in contact with oxygen it becomes a dark purplish red.

The blood is remarkably opaque, as may be seen by placing a thin layer on a piece of glass over the page of a book. This opacity depends on the fact that the blood, as will presently be seen, is not a red

fluid, but owes its colour to the presence of solid red particles or corpuscles which float in a clear pale fluid. The blood has a peculiar smell (halitus) distinct in different animals and man, dependent on certain volatile fatty acids. Its specific gravity varies from 1045 to 1075, the average being 1055. The solid parts (corpuscles) are heavier (sp. gr. 1105) than the liquor sanguinis (1027).

When first shed the blood has a slippery feel, which it soon loses, becoming viscous as it passes into the first stage of coagulation.

Amount of Blood in the Body.

The total amount of blood has been estimated to be from $\frac{1}{13}$ to $\frac{1}{14}$ of the body-weight for an adult man, and somewhat less for a new-born child.

Much difficulty has been found in arriving at an accurate estimation of the amount of blood in the body. In the first place, all the blood cannot be made to flow out of the vessels of an animal when it is killed. Secondly, the quantity and quality of blood are constantly varying with the capacity of the blood-vessels. Thirdly, when slowly withdrawn from the body during life it is rapidly replaced by more fluid passing into the blood vessels. This explains the enormous quantity of blood occasionally reported to be shed in cases of bleeding to death. In these cases, as quickly as the blood is lost, fluid is absorbed by the fine vessels to replace it, so that if the bleeding be gradual the standard quantity is still kept up in the vessels. Thus the very sudden loss of a comparatively small quantity of blood may cause death, whereas, if the bleeding go on sufficiently slowly and gradually, as much or even more in quantity than normally exists in the entire body may escape without fatal result. Of course much of this is fluid which has recently entered the vessels to replace the blood already lost.

Weber's Method.—The per centage of solid matters in the blood is first carefully estimated. The absolute quantity of solids in all the blood drawn is then ascertained and added to the solids obtained by washing out the blood-vessels. Here an error arises from the fact that, in washing out the blood-vessels, much solid matter besides that belonging to the blood is taken from the tissues and thus an excess is found.

Valentine's Method.—A small measured quantity of blood is drawn from a vein and its per-centage of solids accurately estimated; a known quantity of water is then injected into the vessels. When some time has been allowed for proper distribution of the

water a sample of the diluted blood is taken and its solids estimated. The difference in solid contents of the two samples shows the degree of dilution caused by a known quantity of water introduced into blood of ascertained strength, and thus the amount of the diluted fluid (the blood) may be calculated and added to the amount of the first sample to make the absolute quantity.

This method cannot give accurate results, because in the time necessary for the distribution and mixture of the water with the circulating blood much of the former is excreted by the kidneys and skin, and the second sample of blood is more concentrated than should result from such dilution.

Welcker's Method depends upon the estimation of the colouring matter of the blood. He connected the carotid with a small T piece, and allowed the animal to bleed into a bottle in which the blood could be defibrinated by shaking with pieces of glass. One cubic centimetre of this defibrinated blood was carefully measured off and saturated with carbon mon-oxide (CO), which gives a permanent and equally bright red colour. It was diluted to 500 c.c. with distilled water and kept as a standard colour-solution. The blood-vessels of the animal were then washed out with ·6 per cent. solution of sodium chloride until the solution flowing from the jugular vein was colourless. The tissues of the animals were chopped up, steeped in water and pressed. The washings of the vessels and the infusion from the tissues were added together and diluted until they had the same colour-intensity as a layer of the standard solution of the same thickness. Every 500 c.c. of these diluted washings corresponds to 1 c.c. of blood.

By this method the following estimates have been made of the relation of the blood to the body weight:—

Mouse	$\frac{1}{12}$—$\frac{1}{13}$
Guinea Pig	$\frac{1}{17}$—$\frac{1}{22}$
Rabbit	$\frac{1}{15}$—$\frac{1}{22}$
Dog	$\frac{1}{11}$—$\frac{1}{18}$
Cat	$\frac{1}{21}$
Bird	$\frac{1}{10}$—$\frac{1}{13}$
Frog	$\frac{1}{15}$—$\frac{1}{20}$

Only approximate estimates of the distribution of blood in the body during life can be made, since there can be no accurate method of investigation, and the amount varies considerably according as the organ or part is in a state of rest or activity. It is supposed that a

quarter of the entire amount is habitually flowing through each of the following regions :—

1. The heart, great vessels, and lungs.
2. The skeletal muscles.
3. The liver.
4. Skin and other tissues.

Physical Construction of the Blood.

As already stated the blood is not really a red fluid. It is seen with the microscope to be made up of a clear fluid called *plasma* or

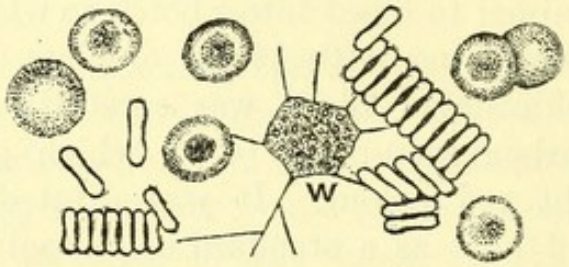


Fig. 95.—Human Blood after death of the elements. The red corpuscles are seen in different positions showing their shape, some also are seen in rolls. Only one white cell (w) is seen, misshapen and entangled in fibrin threads.

liquor sanguinis, which contains an immense number of little disc-shaped bodies—red corpuscles—and a few colourless protoplasmic cells—white corpuscles—so that the living blood may be physically tabulated, giving approximately an estimation of the relative amounts, thus :—

$$\text{Blood} \begin{cases} \text{Plasma or Liquor Sanguinis} \text{ ——— } \frac{3}{5} \\ \text{Solid or Corpuscle} \begin{cases} \text{Red discs} \\ \text{Pale cells} \end{cases} \text{ — } \frac{2}{5} \end{cases}$$

Plasma.

The fluid part of the blood, *plasma* or *liquor sanguinis*, is of a pale straw colour, when pure and free from the colouring matter of the corpuscles, and of slightly less density (v. p. 172).

Unless special precautions have been taken the plasma is altered when removed from the blood-vessels and coagulation of the blood takes place, so that plasma does not come under observation, except when suitable methods are employed to separate it from the corpuscles. It was first separated from the corpuscles by the filtration of

frog's blood to which strong syrup had been added to delay coagulation and destroy the flexibility of the corpuscles, so that they were readily caught in the meshes of the filter and the clear plasma passed through.

To obtain mammalian plasma free from corpuscles it is necessary to use some other method, as the small elastic corpuscles easily run through the meshes of the thickest filter-paper.

The blood of the horse is chosen because it coagulates more slowly than that of most mammals, and delay in the coagulation or postponement of the change in the plasma is the chief object to be obtained. To encourage this delay the blood is drawn from a vein into a cylinder surrounded with a freezing mixture. The cold, however, must not be so intense as to absolutely freeze the blood, for the wished for subsidence of corpuscles could not go on if the blood become solid. It is then left quite motionless for 24 hours, after which time it will be found that the heavy corpuscles have fallen and left a clear supernatant fluid, which is plasma containing some white cells. This can be removed with a cool pipette and passed through an ice-cold filter to remove the cells, then tolerably pure plasma is obtained which soon coagulates at the ordinary temperature.

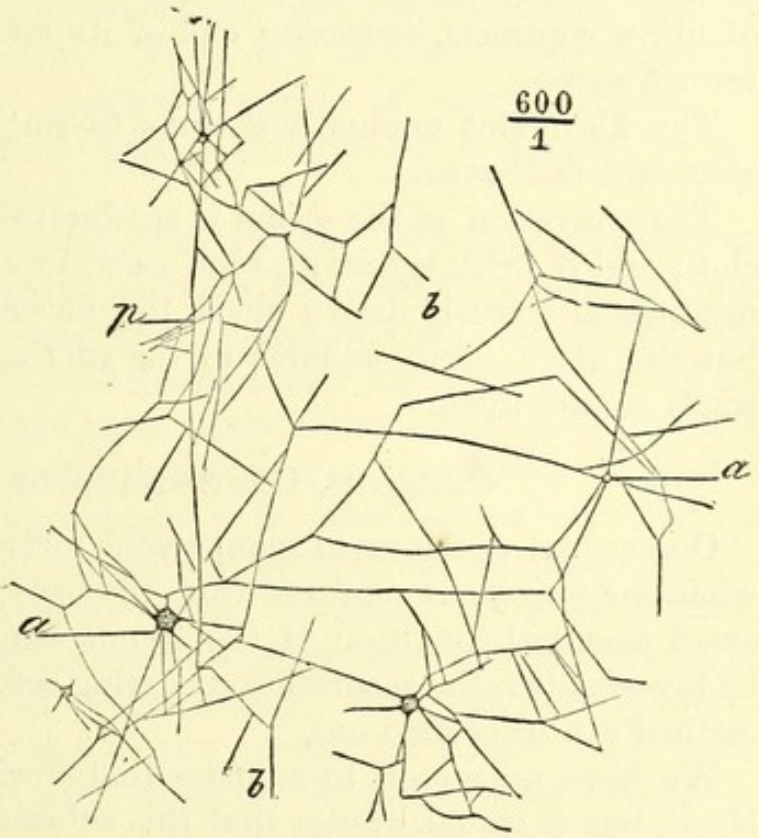


Fig. 96.—Reticulum of Fibrin Threads after staining has made them visible. The network (*b*) appears to start from granular centres (*a*). (Ranvier.)

Another method of checking coagulation consists in letting the blood flow into a 25 per cent. solution of magnesium sulphate (about three volumes of blood to one of the solution). This, if left in a cool place, will not coagulate, and the corpuscles will separate by subsidence from the plasma and salt solution, which form an upper layer

of clear fluid. If the salt be removed by dialysis or weakened by dilution with water, coagulation commences.

The coagulation of plasma can be seen with the microscope to depend upon the appearance of a close feltwork of exquisitely delicate finely granular elastic fibrils which pervade the entire fluid and cause it to set into a soft jelly. The substance forming the meshes is called *fibrin*.

Some time after the plasma has gelatinised, the threads of fibrin break away from their attachment to the vessel in which the coagulum is contained, and owing to their elasticity the general mass of fibrin contracts, squeezing out of its meshes clear drops of fluid termed *serum*.

The fibrin clot gradually shrinks to small size and floats in the abundant fluid serum.

The separation of the serum is accelerated by agitation of the soft clot; and if brisk agitation, such as whipping, be kept up for a few minutes in recently drawn blood, the plasma does not form a jelly, but the fibrin firmly adheres to the stirring rods and at once contracts around them.

Chemical Composition of Plasma.

On account of the rapid spontaneous formation of fibrin and serum when the plasma is removed from the body and allowed to die, the exact chemical condition of the liquor sanguinis during life cannot be investigated, the separation occurring before the simplest chemical method can be carried out.

We have no reason to suppose that fibrin exists normally in the blood, but it would appear that this substance is only formed at the moment of coagulation, its appearance being one of the most obvious of many changes which take place at the time of the death of blood plasma.

The chemical changes comprehended under the term coagulation occurring when plasma is deprived of its means of vitality, and ending in the production of fibrin and serum, are naturally of the first importance in studying the chemical relationships of living plasma. They can best be followed out in the coagulation of plasma when separated from the corpuscles, for (although the stages in the coagulation of blood are the same, the appearance of an insoluble albumin—fibrin—being the one essential in either case), the corpuscles complicate the process and modify the appearance of the clot.

Not only is the fibrin not present as such in the living plasma, but

it requires for its production the presence of other substances which either do not exist in the living plasma, or are there so chemically associated as not to bring about the change which occurs when the plasma dies.

The reasons for believing this are the following. Fluids which sometimes collect by a slow process in the serous cavities of the body, *e.g.*, hydrocele fluid, pleural effusion, &c., if kept quite clean do not generally undergo spontaneous coagulation. If to one of these some serum or recently washed blood-clot be added, coagulation takes place just as in plasma (Buchanan). That is to say, we have here two fluids, neither of which coagulates when left to itself, but which do if mixed together. From each of these fluids a substance can be precipitated by passing a stream of carbon dioxide (CO_2) through the fluids. Both precipitates readily re-dissolve in weak saline solutions.

The solution prepared from the hydrocele fluid causes blood serum to coagulate ; that prepared from the blood serum causes the hydrocele fluid to coagulate ; and when mixed together the mixture of the two solutions coagulates ; while the serum and hydrocele fluid from which the substances have been removed no longer have the power of exciting coagulation in each other or in like fluids. Here, then are two materials : one, obtained in considerable quantity from serum after coagulation, is called *paraglobulin* (Schmidt) or *serum-globulin* (Hammarsten) ; the other, occurring in serous fluids, is named *fibrinogen*. Both these substances are present in the dying plasma of the blood prior to coagulation. They can be obtained both together from the plasma if the plasma be treated with sodium chloride to saturation after either of the precautions already mentioned—viz., the application of cold, or the addition of neutral salt—has been taken to prevent the formation of fibrin. This precipitates a substance which readily dissolves if water be added to weaken the salt solution, and after some time the solution undergoes spontaneous coagulation, while the plasma from which it has been made has lost that power. This *plasmin* (Denis) no doubt is made up of different globulins, chiefly serum-globulin, and fibrinogen, and contains in itself all the necessary "factors" of fibrin formation, but is not at all identical with fibrin, since it readily dissolves in weak saline solutions, like the class of proteids called globulins, while fibrin is quite insoluble in such solutions.

In plasma removed from its normal relationships, both serum-globulin and fibrinogen exist ; but the former in far greater quantity than the latter, since the serum, after the blood-clot is formed, con-

tains no more fibrinogen, while the serum-globulin makes up nearly half the remaining solids.

In preparing fibrinogen and serum-globulin Schmidt found that the more carefully he operated, the weaker and more uncertain their action as fibrin factors became ; and finally he made solutions which, when added together, did not produce coagulation, but which, when added to less pure solutions, gave good firm clots. From this he suspected that a third agent which acted as a ferment was necessary to put into operation the fibrin-producing properties of the other two factors. He further succeeded in preparing the third agent, to which he gave the name of *fibrin-ferment*. By treating serum with strong alcohol the proteids are precipitated ; the ferment is carried down with them, and extracted with water. This extract, added to the mixture of the pure fibrin factors, which previously did not clot, caused rapid coagulation, but not when added to either of them singly.

This material is influenced by those circumstances which affect the activity of ferments in general : it has a minimum, 0° C., optimum, 38° C., and maximum 80° C. temperature of activity, with various gradations of rapidity of action between each, and is destroyed if heated above 80° C. An active solution having the properties of the ferment can be extracted from whipped fibrin preserved in alcohol by an 8% solution of common salt (Gamgee).

Hammarsten thinks that the serum-globulin is not indispensable to the formation of fibrin, because (1) a solution of fibrinogen may be made to coagulate without its presence ; (2) the *fibrinoplastic* property of serum-globulin is shared by casein and calcic chloride ; (3) and is absent from pure serum-globulin, (4) such as is present in hydrocele fluid which does not coagulate on the addition of fibrin ferment.

The source of fibrin is still a question of much difficulty, and will be further discussed with the question of blood coagulation within and without the vessels, after the morphological elements have been described.

Fibrin.

Fibrin may be procured either from plasma or blood by whipping, and then washing the insoluble product with water. When fresh it has a pale yellow or whitish colour, a filamentous structure, and is singularly elastic. It is not soluble in water, weak saline solution, or ether. Alcohol makes it shrink by removing its water. When quite dry it is brittle and hard, and can be reduced to a powder. It

swells in 1 per cent. hydrochloric acid, and if warmed is converted into acid albumin and dissolved.

The amount formed varies very much even in the blood drawn from the same animal at the same time, but is always very small compared with the size of the blood-clot. It never reaches as much as 1 per cent., commonly varying from 0·1 per cent. to 0·3 per cent. of the entire mass of bloed.

Serum.

This name is given to the clear fluid which oozes out of the clot of plasma. It only differs from the latter in its chemical composition in so far that fibrin is separated from it. Though chemically this is a slight difference it signifies the change from a complex living body (blood-plasma) into a solution of dead albumins, &c.

Serum is a clear straw-coloured alkaline fluid of 1028—1030 sp. gr., holding in solution different organic substances and some inorganic salts. After a full meal the serum is said to be slightly milky from the presence of finely divided fat.

It contains about 9 per cent. of solid matters, of which a large proportion, 7 per cent., are proteids. Of these the most abundant is (1) serum-albumin (about 4 per cent. in man), a solution of which becomes opaque at 60° C., and coagulates at a heat of 73°—75° C. The proteid next in importance is (2) serum-globulin or paraglobulin (about 3 per cent. in man), which has already been mentioned. It may be precipitated imperfectly by CO_2, or completely by magnesium sulphate. (3) Serum casein has been obtained from serum by careful neutralisation with acetic acid after the removal of the serum-globulin by CO_2. This is said to be serum-globulin which has failed to come down with the CO_2. (4) Neutral fats in a state of fine subdivision are present in a variable quantity: also (5) lecithin; (6) traces of sugar; (7) various products of tissue change—kreatin, urea, &c.; and (8) inorganic salts, viz., sodium chloride, about 5 per cent., and sodium carbonate, which probably existed in the blood as sodium hydric carbonate. There is also a small quantity of potassium chloride. But it should be remembered that about ten times more sodium than potassium salts exist in the serum, and probably in the blood-plasma.

CHAPTER XIV.

BLOOD CORPUSCLES.

THE relative number of red discs to the colourless cells is said to be, on the average, 350 to 1. This is true of the blood drawn from the fine vessels by puncture. While in the vessels the blood must contain a greater proportion of the colourless cells, for by the ordinary method of obtaining blood for examination, they do not flow out of the punctured capillaries as readily as the red discs, and many of them are said to become disintegrated very shortly after they are removed from the circulation. Although the number of red discs normally alters but little, on account of the constant changes occurring in the number of the white cells, the proportion of white to red varies much. It has been found to differ according to the observer, the situation, and other circumstances, as shown in the following table, which gives the number of red corpuscles to one colourless cell :—

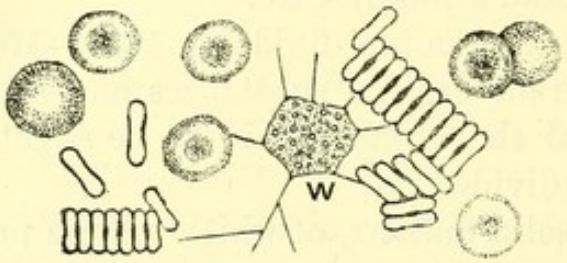


Fig. 97.—Human Blood after death of the elements. The red corpuscles are seen in different positions showing their shape, some also in rolls. Only one white cell (w) is seen, misshapen and entangled in fibrin threads.

	Red. White.
Observer's estimate of normal proportion :—	
Welcker	335—1
Moleschott	357—1
In various parts of the circulation :—	
Splenic vein	60—1
Splenic artery	2260—1
Hepatic vein	170—1
Portal vein	740—1

According to age or sex :—	Red. White.
Girls	405—1
Boys	226—1
Adult	334—1
Old Age	381—1

According to general conditions :—	
When fasting	716—1
After meal	347—1
During pregnancy	281—1

In a disease of the spleen and lymphatic glands called Leucocythemia there may appear to be nearly as many white cells as red discs. Here, however, the red discs are deficient, while the colourless cells are multiplied.

The Colourless Corpuscles.

The colourless cells of the blood, commonly called the white corpuscles, differ in no essential respect from the pale round cells which are found in most of the tissues of the body. They exist in large numbers in that fluid, namely, the lymph, which is drained back from the tissues into the blood, and occupy a great part of the lymphatic glands and spleen. They are often spoken of as lymphoid cells, leucocytes, indifferent, or formative cells, on account of their being so widely distributed throughout the tissues.

When fresh blood is examined with the microscope these cells can generally be seen adhering to the glass slide or cover-glass and lying singly, apart from the groups of red discs. They can be recognised by their absence of marked colour, finely granular structure, spherical shape, and the nuclei which may often be recognised near the centre of the cell. Though not always visible in fresh preparations the nuclei can be brought to light by the action of many reagents —*e.g.*, acetic acid. If examined while being moved by the blood-current in the capillary vessels, they are seen to pass slowly along in contact with the vessel wall, while the red corpuscles rush rapidly past them down the centre of the channel (Fig. 98). This may partly be due to their peculiar adhesiveness, which also causes them to stick to the glass slide, whilst the red discs are washed away when a gentle stream of saline solution is allowed to flow under the cover-glass. These cells show all the manifestations of activity characteristic

of independent living beings. If kept in a medium suitable to them, and at the temperature of the body, they will soon be seen to alter their appearance; their outline becomes faint, they are no longer spherical, but very irregular in shape, and constantly change their form by sending out and retracting processes, by means of which they change their position, so that they may be said to perform locomotion. These movements are rendered more active by a slight increase of temperature, and are checked by cold. For continued observation about 38° C. is the best temperature for mammalian blood. The blood of the Frog is generally used to see the motion of the white corpuscles, as warming is unnecessary in the case of cold-blooded animals. They respond to many other influences, such as electricity, &c., even for a considerable time after removal from the body.

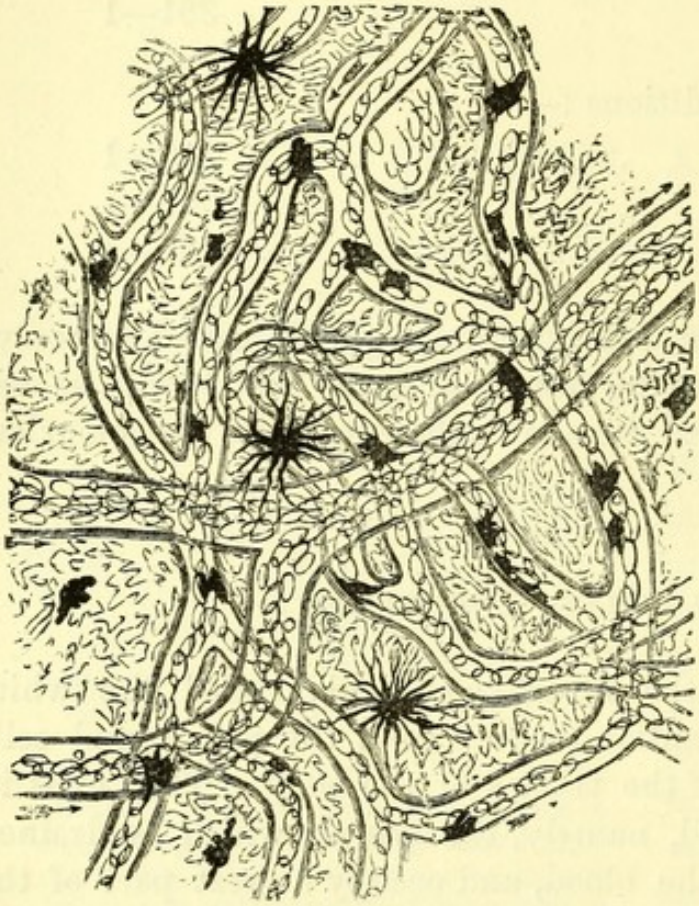


Fig. 98.—Vessels of the Frog's Web.

(*a*) Trunk of vein, and (*b b*) its tributaries passing across the capillary network. The dark spots are pigment cells.

No doubt they continually absorb fluid nutriment from the surrounding medium, as is shown by the effect of poisons on them; and, by the repeated contractions and relaxations of parts of their substance in the form of pseudopodia, they appear to take into the inner parts of the protoplasm solid particles, which after some time are ejected after the manner of the small unicellular animals known as amœbæ (p. 60).

While in motion in the circulation none of these amœboid movements appear to take place, but when an arrest of the flow of blood in the capillaries occurs they not only change their form, but also their position; and if there be no onward flow of blood for some little time, they creep out of the capillaries, passing through the

delicate vessel-walls. This emigration of the blood-cells is possibly a common event when a tissue is in need of textural repair. When excessive it forms one of the most striking items of the series of events occurring in inflammation.

These cells differ much in size; generally they are somewhat larger than the red discs. Nothing like a cell-wall can be seen to surround them, and from the movements above described it would appear certain that they are free masses of active protoplasm.

The number of white cells that can be collected is too small to allow of accurate chemical analysis, but there is no reason to suppose that they differ from other forms of protoplasm.

Origin of the Colourless Blood-cells.

Since such an ordinary circumstance as a hearty meal can materially influence the numbers of the white corpuscles, it would appear that they must be usually undergoing rapid variations in their number—probably by their being constantly used up and periodically replaced by new ones. The places in which they occur in greatest number are the lymphatic glands, the spleen, and the lymph follicular tissue in the intestinal tract.

There is no doubt that the lymph contains a much larger proportion of these cells after it has passed through the lymph-glands, and the blood coming from the spleen contains an excessive proportion of them.

It is then not unreasonable to suppose that many of the white cells found in the blood have their origin in these organs.

They may also be developed from similar cells in any tissue, but their reproduction by *division*, other than that which probably occurs in the lymph follicles where it cannot be seen, is a circumstance of the greatest rarity, and few observers have been fortunate enough to witness the phenomenon.

The destiny of the white blood-cells is probably manifold. From the readiness with which they escape from the capillaries and wander by their amœboid movement through the neighbouring tissues to reach any point of injury, it would appear that they take an active part in the repair of a tissue whose vitality has in any way suffered. During the growth of all tissues these cells seem to contribute active agents to their formation; thus in the formation of bone it has been stated that escaped blood-cells or their immediate offspring

help to lay down the calcareous material, and some even settle themselves as permanent inhabitants of the lacunæ.

Further, they are in all probability the means of renewing the red discs. Their protoplasm either takes up the colouring matter from its surroundings, or forms it within itself from suitable ingredients. Certain it is that cells are found which are recognisable as white blood cells which have more or less of the red colouring matter embedded in their substance. As this increases the cell gradually loses its distinctive characters, and assumes those of a red corpuscle. Such elements, it will be seen, are common in the spleen and the blood leading from it.

The Coloured Corpuscles.

The red discs were discovered in the human blood by Leuwenhoek, about 1673. They give the red colour which characterises the blood of all vertebrated animals (except the amphioxus), but are not found in the blood of the invertebrata, which only contains colourless cells. When the blood of the invertebrates has a colour, it owes it to the fluid, not to the corpuscles. The individual discs when viewed singly under the microscope appear to be pale orange, but when in masses the red becomes apparent.

The shape of the corpuscles differs in different classes of animals. In man and all other mammalia they are discs, concave on each side, and rounded off at the margin. The only class of mammals which forms an exception to this rule is the camelidæ, whose red corpuscles are elliptical in shape, like those of non-mammalian vertebrates.

The corpuscles of birds, amphibia and fish are flattened elliptical plates, slightly convex on each side, and containing a distinct oval nucleus in their centre.

The size of the corpuscles varies greatly in different classes of animals, but is strikingly constant in the same class. A glance at the following diagram, in which the corpuscles are drawn to scale, will give an idea of their relative sizes, in examples of the different classes of animals, and will make the following points more rapidly obvious than mere description.

The size of the animal has no general relation to the size of the corpuscles. The human red discs are of a fair average size when compared with those of other mammals, and therefore man's blood cannot be distinguished from that of the other mammalia.

The mammalian corpuscles are, on the whole, small when compared with those of the other vertebrates. The batrachians are distin-

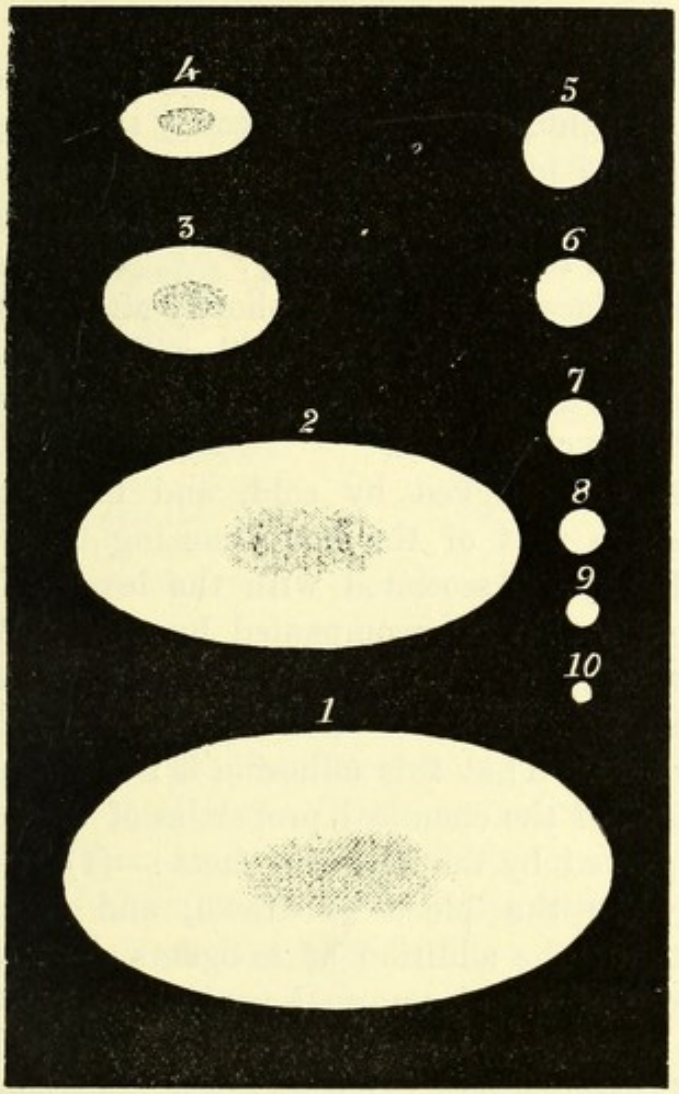


Fig. 99.—Diagram of the relative sizes of red corpuscles of different animals. The measurements below are in fractions of a millimetre.

1. Amphiuma . . . $\frac{1}{16} \times \frac{1}{30}$	6. Man . . . . . $\frac{1}{126}$
2. Proteus . . . . $\frac{1}{18} \times \frac{1}{44}$	7. Dog . . . . . $\frac{1}{139}$
3. Frog . . . . . $\frac{1}{45} \times \frac{1}{66}$	8. Horse . . . . . $\frac{1}{181}$
4. Pigeon . . . . $\frac{1}{225} \times \frac{1}{120}$	9. Goat . . . . . $\frac{1}{253}$
5. Elephant . . . $\frac{1}{108}$	10. Muskdeer . . . . $\frac{1}{483}$

guished by the great size of the corpuscles. Those of the Amphiuma tridactylum are visible to the naked eye.

The following measurements are given by Welcker for the human discs :—

Diameter . ·0077 of a millimetre (7·7μ *) = $\frac{1}{3200}$th of an inch.
Thickness . ·0019 of a millimetre (1·9μ) = $\frac{1}{12400}$th of an inch.
Volume ·000000077 of a cubic millimetre.
Surface . ·000128 of a square millimetre.

* The Greek letter μ is used by histologists to denote $\frac{1}{1000}$ of a millimetre, which is taken as a convenient unit of measurement.

The last measurement would give a surface of about 2,816 square metres for the corpuscles of an adult. A surface of 11 square metres is exposed every second in the lungs for the absorption of oxygen.

When circulating in the vessels, or immediately after removal, the red corpuscles are very soft and elastic, being bent and altered in shape by the slightest pressure, and easily stretched to twice their diameter. But the moment pressure or traction is removed, they return to their normal biconcave disc-shape if the medium in which they lie continue of the normal density.

Changes take place in the blood shortly after it is removed from the body, which seem to be associated with the loss of function (death) of the red discs, as shown by their rapid destruction if re-introduced into the circulation.

The changes are checked by cold, and facilitated by heat, a temperature above that of the body causing them to take place almost immediately. Associated with the loss of function of the discs is observed a change accompanied by an apparent increase of adhesiveness, which causes them to stick together, commonly adhering by their flat surfaces, so as to form into rolls, like so many coins placed side by side. That this adhesion is not a mere physical process, independent of the chemical properties of the corpuscles themselves, seems proved by the following facts :—(1) It does not occur immediately when the blood is drawn, and disappears after a few hours without the addition of re-agents ; (2) while the blood is in the living vessels under normal conditions there is no adhesion, but this soon appears when any standstill in the circulation takes place—as in inflammation ; (3) it does not occur when saline solutions are added to the blood. It seems to be dependent upon a peculiar property of the discs, which only exists for a time coincident with the changes that accompany the death of the blood and the appearance of fibrin.

The shape of the discs changes when the density of the medium in which they are suspended is altered. When the density is reduced, as by the addition of water, they swell and become spherical, and break up the *rouleaux*, the colouring matter at the same time becoming dissolved in the medium. (Fig. 100.) When the density is increased by slight evaporation, or the addition of salt solution about 1 per cent., they cease to be concave, and become *crenated* or spiked like the green fruit of the horse-chestnut. (Fig. 101.) The addition of strong syrup causes the corpuscles to shrivel and assume a great variety of peculiar bent or distorted forms. (Fig. 102.) Elevation of temperature or repeated electric shocks causes a peculiar

change in shape, but since the change is associated with the death of the element, it cannot be attributed to vital activity comparable with that seen in the white cells.

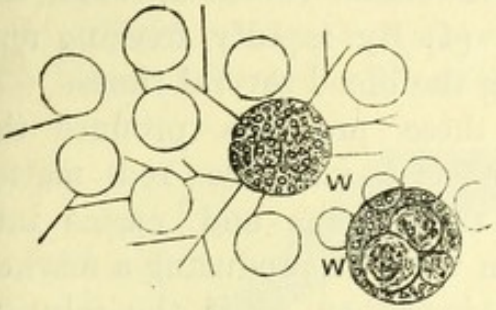


Fig. 100.—Microscopic appearance of the blood after the addition of distilled water. Red Corpuscles become colourless or pale, separate, and spherical. The white are seen to be swollen round and granular with clear nuclei.

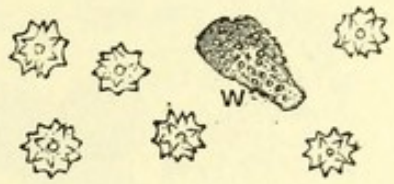


Fig. 101.—Showing effect of evaporation. Six Red Corpuscles crenated. (w) White cell changing shape.

The discs show no signs of structure under the microscope : they are perfectly homogeneous, transparent bodies of a pale orange colour, all efforts to demonstrate the limiting membranes, formerly supposed to surround them, having failed. Their behaviour when certain reagents are added to the blood shows that the corpuscles have two constituents : (1) the colouring matter, *Oxyhæmoglobin ;* and (2) the *Stroma.* The colouring matter may be removed from the corpuscle, as above stated, by water, and leaves a perfectly colourless transparent foundation or groundwork, which appears to be in some way porous, so as to hold the colouring matter in its interstices. The effect on the naked-eye appearance of the blood produced by the removal of the colouring matter from the stroma is to alter the colour and increase the transparency of the fluid. The oxyhæmoglobin now forms a transparent dark-red, *lakey* solution, and the corpuscles, being quite colourless, are practically invisible. This transparency of the fluid does not depend on any change in the oxyhæmoglobin, but merely on its being dissolved out of the discs, which become transparent and can no longer reflect the light. This process, which is commonly spoken of as rendering the blood "lakey," may be brought about by the following means. (1) The addition of about $\frac{1}{4}$ its bulk of distilled

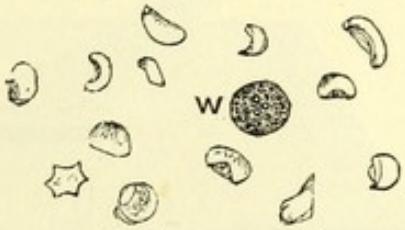


Fig. 102.—Red Corpuscles, shrivelled by the addition of strong syrup. (w) White Corpuscle.

water, to wash the colouring matter out of the stroma, which may then be rendered visible by a weak solution of iodine. (2) By the addition of chloroform, ether, or alkalies. (3) By passing repeated strong induction shocks through the blood. (4) By rapidly freezing and thawing the blood several times.

Fig. 103.—Blood Corpuscle after the addition of tannic acid. (½%.)

All these processes produce the same effect; viz., the red matter leaves the stroma and passes into solution without producing a marked change in either, as if the solution depended upon the destruction of some vital relationship between the stroma and the oxyhæmoglobin which prevented the diffusion of the latter in the living blood.

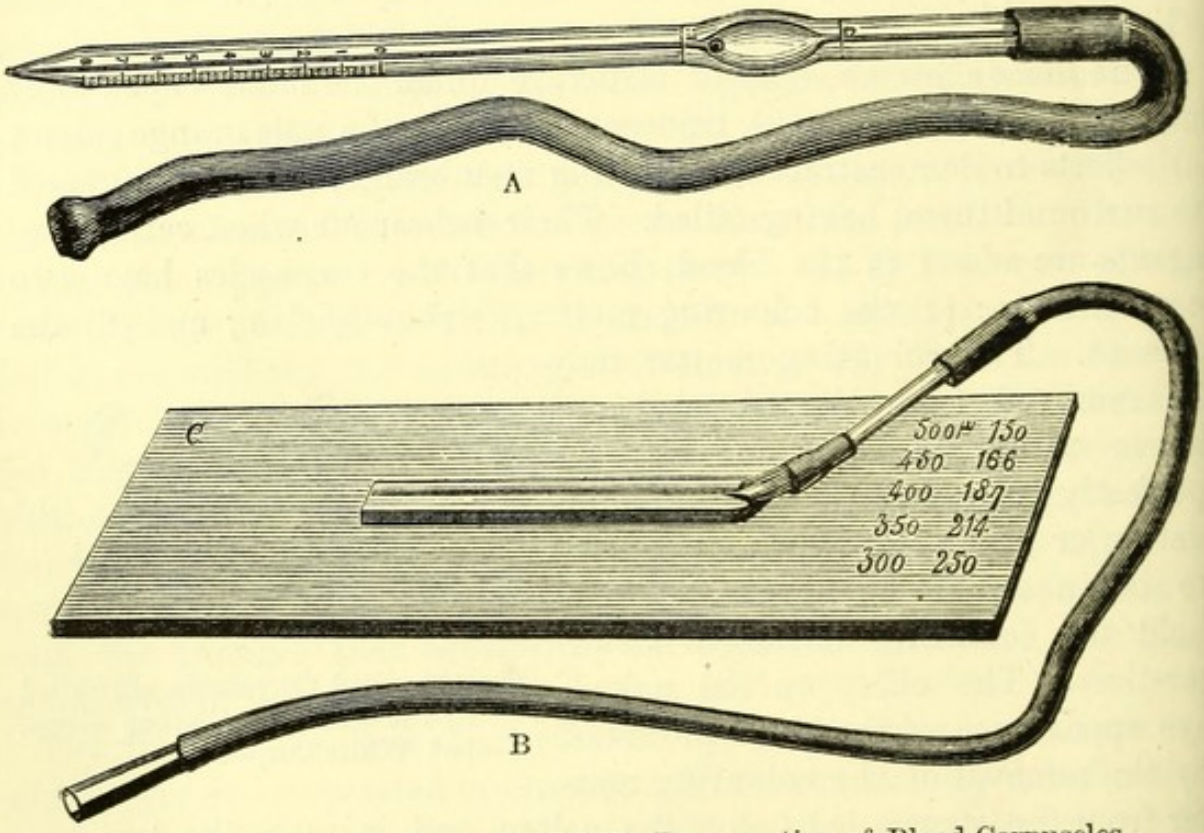


Fig. 104.—Malassez' Apparatus for the Enumeration of Blood Corpuscles.

A. Measuring and mixing pipette. B. Flattened and calibrated capillary tube.

Solutions of urea, bile, acids and heat of about 60° C. seem to destroy the discs, and thus remove the colouring matter. Carbolic, boracic, and tannic acids cause the colouring matter to coagulate and localise itself either at the centre or margin of the corpuscle. (Fig. 103.)

The number of discs in the blood of man is enormous, namely, in a cubic millimetre of blood, about 5 millions for males, and

4½ millions for females, or about 250,000 millions for one pound of blood. The number varies much, not only in disease, but also as a result of the many physiological processes, such as changes in the amount of plasma, brought about by pressure-differences, &c.

In order to count the corpuscles the following method is employed. The blood is diluted with artificial plasma to 100 or 1,000 times its

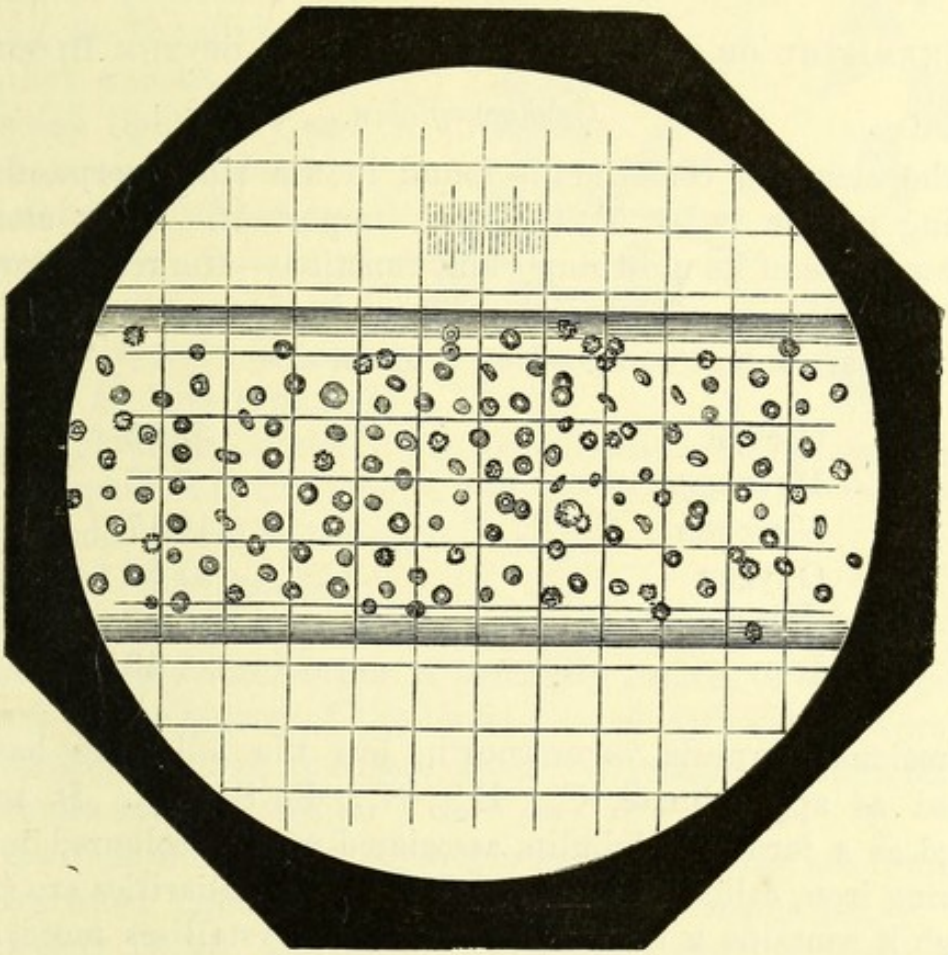


Fig. 105.—The appearance presented by the Capillary Tube of Malassez' Apparatus when filled with diluted blood and examined under a microscope magnifying 100 diameters, provided with an eye-piece micrometer.

volume, and the corpuscles in a portion of the mixture carefully measured off by a capillary tube, and counted. This operation requires great care and delicate apparatus. One of the best-known methods is that of Malassez, the details of which are as follow :—

Blood is drawn into the capillary tube of a specially prepared delicate pipette (Fig. 104, A) up to a mark which indicates $\frac{1}{100}$ part of the capacity of the pipette. This known quantity of blood is then washed into the bulb of the pipette by drawing up artificial serum to fill the bulb, where the fluids are mixed by shaking about a glass bead contained in its cavity. Some of this mixture is then allowed

to pass into a flattened capillary tube of known capacity fixed on a slide, and the number of corpuscles in a given length of this tube is carefully counted at two or three places. The important question, how much oxyhæmoglobin exists in a given sample of blood, can be determined by diluting some of it until the colour equals that of a standard solution of known strength.

Chemistry of the Colouring Matter of the Blood.

Oxyhæmoglobin.

Of the chemical constituents found in the blood corpuscles, the colouring matter is by far the most important. To it alone the blood owes one of its most important functions—the respiratory.

Oxyhæmoglobin is a chemical compound of great complexity, of which the per-centage composition is given as—

Carbon	53·85
Hydrogen	7·32
Nitrogen	16·17
Oxygen	21·84
Sulphur	·39
Iron	·43

Its rational formula is unknown, but the following has been proposed as approximate, $C_{600}\ H_{960}\ N_{154}\ Fe\ S_3\ O_{179}$. It may be regarded as a form of globulin, associated with a coloured material containing iron, called Hæmatin. Its chief peculiarities are (1) that although it contains a colloid substance, it crystallises more or less readily in all vertebrates when removed from the stroma of the corpuscles; (2) the considerable amount of iron it contains (0·4 per cent.); (3) the remarkable manner in which it is combined with oxygen to form an unstable compound; and (4) the ease with which it yields its oxygen to the tissues and takes it from the air.

The readiness with which the *oxyhæmoglobin crystals* are formed varies much in different animals and under different circumstances, as may be seen from the following list—

Most readily—rat, guinea pig, mouse.
Readily—cat, dog, horse, man, ape, rabbit.
With difficulty—sheep, cow, pig.
Not at all—frog.

The presence of oxygen causes the crystals to form more rapidly,

so that a stream of oxygen passed through a strong solution of hæmoglobin causes small crystals of oxyhæmoglobin to form.

The crystals always belong to the rhombic system, being most frequently plates (man, &c.) and prisms (cat), and rarely tetrahedra (guinea pig) and hexagonal plates (squirrel).

The colour of the crystals and their solution varies according to the light by which they are looked at. By reflected light they are bluish red or greenish in colour, and by direct light, scarlet.

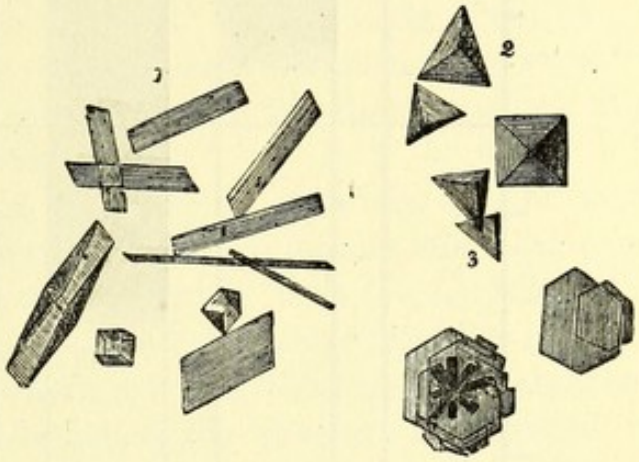


Fig. 106.—Crystals of Hæmoglobin from different animals, showing the variety in form of crystals.

The *preparation of oxyhæmoglobin* crystals is accomplished by first separating the colouring matter from the corpuscles by freezing, or the addition of water or ether, and then rendering it less soluble by evaporation, cold, and the addition of alcohol.

For microscopic observation it generally suffices to kill a rat with ether, and expose a drop of the blood diluted with distilled water on a slide until half dried, and then cover. Crystals appear in the fluid as it becomes concentrated.

The combinations which hæmoglobin enters into are numerous and throw much light upon the function of the corpuscles.

As already stated, the colouring matter, when exposed to the air, combines with oxygen to form a loose chemical compound called oxyhæmoglobin. This is the condition in which the colouring matter of the blood is generally found. Although so prone to combine with oxygen, the oxyhæmoglobin very readily parts with some of it. In the circulation it is always united with oxygen, normally leaving the lungs in a state of saturation. On its way through the capillaries of the tissues, some of it parts with a little of its oxygen, becoming partially reduced (hæmoglobin), but even the most venous blood always contains some oxyhæmoglobin.

The oxygen can be removed by reducing the pressure under an air pump, or by exposing the solution to a mixture of nitrogen and hydrogen. Various reducing agents rob the oxyhæmoglobin of its oxygen ; and if blood or a solution of oxyhæmoglobin be sealed in a glass tube so as to exclude the air, the loose oxygen is taken up by

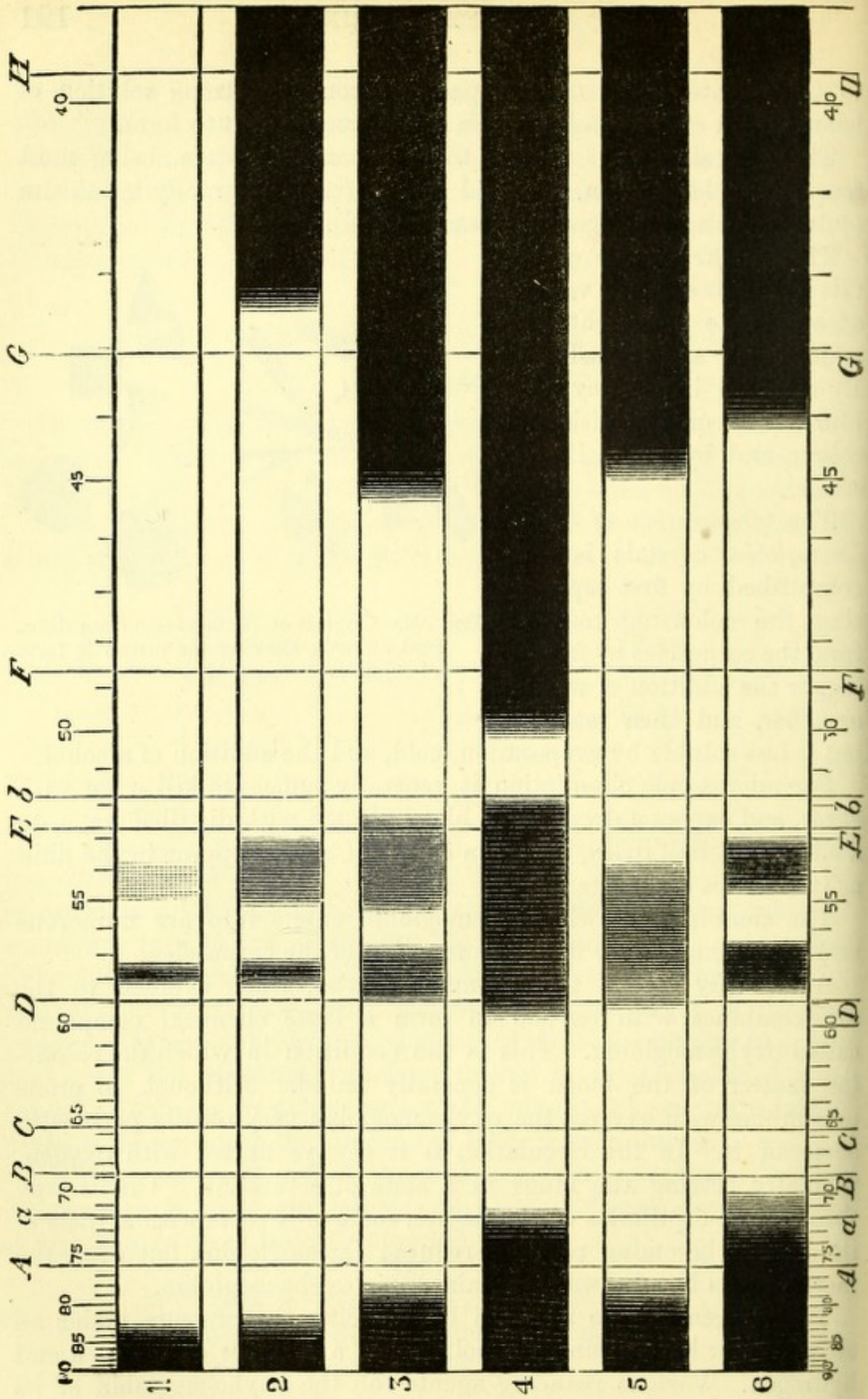


Fig. 107.—The Spectra of Oxyhæmoglobin, Reduced Hæmoglobin, and CO-hæmoglobin (Gamgee.)

1, 2, 3, and 4. Oxyhæmoglobin increasing in strength or thickness of solution.
5. Reduced Hæmoglobin. 6. CO-hæmoglobin.

some of the other constituents of the blood, and the oxyhæmoglobin becomes gradually reduced to hæmoglobin, after which it undergoes no further change or decomposition. The reduction in the sealed tube depends on the putrefactive changes in the proteids, and may be prevented by careful aseptic precautions. If the reduced hæmoglobin be shaken for a few moments with air, the bright colour characteristic of oxyhæmoglobin soon reappears, and if the reducing agent be not injurious to the blood, the reduction and reoxidation may be repeated several times, the hæmoglobin going through the changes which take place in it during normal respiration.

The union of oxygen with hæmoglobin solutions is not mere absorption of the oxygen by the liquid, but a definite chemical combination. This is proved by the following facts :—(1.) When the pressure is removed the oxygen does not come away from the solution in accordance with the law which governs the escape of absorbed gas, but all comes off suddenly when the pressure is lowered to about $\frac{1}{12}$ of an atmosphere (*vide* p. 197). (2.) The two substances give a different absorption band when examined with the spectroscope. The reduced hæmoglobin gives one wide diffuse band, which lies between the D and E lines of the solar spectrum, and much of the violet end is cut off. The single band, which is characteristic of reduced hæmoglobin, is replaced by two when the hæmoglobin combines with oxygen—one broad band in the green near E, and a narrow one, more clearly defined, in the yellow close to the D line ; both bands lie between D and E. With strong solutions the spectrum is darkened at either extremity, and the two bands become wider and tend to fuse into one. (3.) Further, the oxygen may be replaced by other substances which unite with the hæmoglobin. One of the most important of these is carbonic oxide, which forms a much more stable compound with hæmoglobin than oxygen. It is of a bright cherry-red colour, and has two absorption bands in the spectrum very like those of oxyhæmoglobin ; that in the yellow is, however, removed a greater distance from the D line towards the violet end.

It is this compound which is formed in poisoning with carbonic oxide. The CO occupying the place of the oxygen, destroys the function of the blood corpuscles. CO-hæmoglobin may be distinguished from O-hæmoglobin by not being reduced by reagents greedy of oxygen, and by the bright red colour which persists when 10 per cent. solution of caustic soda is added, and the mixture heated. O-hæmoglobin gives a muddy-brown colour under the same treatment.

Methæmoglobin.

When a solution of oxyhæmoglobin is exposed to the atmosphere for a few days its colour changes to a dingy brown, and it takes up more oxygen than it previously contained. The new product is called *methæmoglobin*. The oxygen is more firmly combined than in the oxyhæmoglobin, so that it cannot be removed by passing other gases (CO, &c.) through the liquid, or by exhaustion with an air-pump. Methæmoglobin gives an absorption spectrum which differs from that of oxyhæmoglobin in having only a single band, and from that of reduced hæmoglobin in that the single band is placed more to the red side of the spectrum, *i.e.*, between the lines C and D. This substance can also be formed by the addition of potassium permanganate or alkaline nitrites to hæmoglobin. A solution of methæmoglobin, though unaltered when placed in vacuo, may be reduced to hæmoglobin by ammonium sulphide. It then regains its red colour, shows the spectrum of reduced hæmoglobin, and when shaken with air reforms oxyhæmoglobin.

Decomposition of Hæmoglobin.

Hæmoglobin may easily be broken up into two constituents—namely, (*a*) a colourless substance which is nearly related to the class of proteids called globulin, and (*b*) a blackish red amorphous material called *Hæmatin*, which contains all the iron of the hæmoglobin.

This change is brought about by whatever causes the coagulation of albumin, such as the addition of acids, strong alkalies, and heat above 70° C.

Hæmatin, &c.

Hæmatin is a secondary product, being the result of the oxidation of a substance called *hæmochromogen*, which is the first outcome of the decomposition of the hæmoglobin by acids or strong alkalies. Hæmochromogen or *reduced hæmatin*, as it may be called, can be obtained from hæmatin by acting on that body with ammonium sulphide, but it can only be preserved in an atmosphere of hydrogen or nitrogen, as it immediately takes up oxygen to form hæmatin on exposure to the air. The formula $C_{68}H_{70}N_8Fe_2O_{10}$ has been given for hæmatin. It dissolves in weak alkaline and acid solutions, but not in water or in alcohol.

Hæmatin is readily prepared by mixing acetic acid with a strong

solution of hæmoglobin, which becomes a dark-brown colour. The dark hæmatin can be removed by ether. But if the acid used be strong, the solution of hæmatin is found to be free from iron. This iron-free hæmatin is called hæmatoporphyrin or *hæmatoin*. If now the acid hæmatin solution be saturated with ammonia, the iron again becomes united with the hæmatoin, forming *alkali-hæmatin*.

Hæmin.

Hæmatin unites with hydrochloric acid to form a crystallisable body called *hæmin* or hydrochlorate of hæmatin (Teichmann's crystals).

If blood or dry hæmatin be mixed with a small quantity of common salt, a drop of glacial acetic acid added, and the mixture boiled, small characteristic crystals appear which have been found to be produced by the union of two molecules of hydrochloric acid with the hæmatin.

Fig. 108.—Hæmin Crystals.

The formation of these crystals is very easily accomplished with a small quantity of old dried blood; therefore this substance becomes, in medico-legal inquiries, an important test for blood-stains.

Crystals of a substance called *Hæmatoidin* are formed in old blood-clots retained in the body. It does not contain any iron, and has the chemical formula $C_{32}\ H_{36}\ N_4\ O_6$. It is probably identical with *bilirubin*, one of the colouring matters found in bile.

Globin.

This name has been given by Preyer to the proteid part of the hæmoglobin, on account of its slightly differing from globulin, though it resembles it in being precipitated by the weakest acids, even carbon dioxide, and it leaves no ash on ignition.

Chemistry of the Stroma.

The stroma forms only about 10 per cent. of the solid parts of the corpuscles, the rest being hæmoglobin. The proteid basis of the stroma is probably made up of a globulin, also containing lecithin, cholesterin and fats in minute proportions. There is little more than one-half per cent. of inorganic salts in the red blood corpuscles, of which more than half consists of potassium phosphate and chloride.

Development of the Red Discs.

In the early days of the embryo the blood-vessels and corpuscles appear to be formed at the same time from the middle layer of the blastoderm (mesoblast). They first consist of round, nucleated, colourless cells, which subsequently become coloured, gradually lose their nucleus, and assume the characteristic shape of the red corpuscles, the rest of the original mass of protoplasm remaining as a rudimentary blood-vessel.

In the later stages of embryonic life the red corpuscles are said to be formed in the liver, possibly out of protoplasmic elements which are made in the spleen and thence carried to the liver by the portal circulation.

In the connective tissue of rapidly growing animals—tadpole (Kölliker), rabbit (Ranvier), rat (Schäfer)—certain cells can be seen connected in the form of a capillary network, and within the protoplasm of these cells red colouring matter is developed, and the particles of colour can soon be recognised as characteristic blood corpuscles, arranged in rows within the newly-formed networks. Thus isolated small networks of capillaries, consisting of a few meshes filled with blood corpuscles, are formed independently of the general circulation.

These corpuscles and their hæmoglobin are manufactured by isolated protoplasmic elements in the connective tissue, and subsequently added to the general mass of blood by the growth of the network bringing it into continuity with the neighbouring vessels.

In the adult the formation of red blood corpuscles is much less active, but never ceases to take place in health, for the corpuscles must be renewed as they become worn out, and incapable of performing their function. This reproduction can go on with considerable rapidity, as we see after severe hæmorrhage, when the normal richness in hæmoglobin and corpuscles is soon regained. Their formation is, however, probably confined to a few special organs—spleen, liver, red medulla of bones—where transitional forms are found in such numbers as to point to the probability of the red corpuscles being the offspring of the colourless cells, whose protoplasm either manufactures anew or collects the necessary hæmoglobin, and then loses its nucleus and ordinary cellular characters.

We can only guess at the fate of the discs, but there are many things which point to the spleen as the organ in which they are destroyed. In the spleen an enormous number of protoplasmic elements are produced, and the blood comes into relationship with

the nascent cells in a way unknown in any other part of the body. Further, various unusual elements, some like altered red corpuscles, others like white cells enveloping hæmoglobin, are found in this organ.

The blood corpuscles on coming to the spleen are possibly submitted to a kind of preliminary test of general fitness, some elements of the spleen pulp having the faculty of examining their condition and deciding upon their fate. Many, no doubt, pass the trial without any change, being found in good working order. Others that are found totally unfit are broken up, and their effete hæmoglobin carried to the liver to be eliminated as bile pigment. Some possibly undergo a form of repair : a white cell taking charge of a weakly disc renews its stroma, adds to its hæmoglobin, and carries it through the final proof in the liver, where it is chemically refreshed before going to the lungs for the load of oxygen which it has to carry to the systematic capillaries.

The Gases of the Blood.

These are present in two conditions : (1) dissolved in accordance with well-established physical laws,* and (2) chemically combined. But since those present in the latter state are but loosely combined they may be separated by the same means as the former, and thus the oxygen, carbon dioxide, and nitrogen can all be removed by reducing the pressure with the air-pump. For this purpose a mercurial pump must be used, by means of which a practically perfect vacuum can be formed and all the gases obtained in a manner which facilitates further analysis. Together they are found to measure about 60 volumes for every 100 volumes of blood.

Oxygen.—The amount of oxygen in the blood is found to vary much with circumstances. In arterial blood the quantity is much more constant, and always exceeds that in venous blood. It is

* I. At the same temperature the *volume* of a gas varies inversely with the pressure, so that with twice the pressure a given volume of a gas is twice the *weight*.

II. A given liquid absorbs the same *volume* of a given gas, to which it is exposed, independent of the pressure exercised by that gas.

III. Therefore the amount *by weight* of gas absorbed by a liquid, at a given temperature, depends directly on the pressure, being *nil* in vacuo.

IV. The weight of a given volume of a gas decreases and the coefficient of absorption of a liquid diminishes, as the temperature increases.

V. Therefore the amount of gas absorbed is in inverse proportion to the temperature, being practically *nil* at boiling point.

estimated (at 0° C. and 760 mm. pressure) that every 100 volumes of arterial blood yield 20 volumes of oxygen, whilst the volume of oxygen in venous blood varies from 8 to 12 per cent.

The oxygen which comes off in the Torricellian vacuum exists in the blood in two distinct states :—(1) a very small quantity simply absorbed, — about as much as water absorbs under atmospheric pressure ; (2) chemically combined, in which state nearly all the oxygen exists, and forms with the hæmoglobin the loose combination called oxyhæmoglobin. This oxygen therefore does not follow the laws of absorption by leaving the blood in proportion as the pressure is reduced, but when a certain point of reduction of pressure (20—30 mm. mercury, according to the temperature) is reached, the oxygen comes off almost completely.

Carbon Dioxide (CO_2).—The amount of carbon dioxide also varies more in venous than in arterial blood, for under certain circumstances (suffocation) it may rise to over 60 volumes per cent., although ordinary venous blood on an average contains only 46 volumes in every 100 of blood. On the other hand, the amount of this gas in arterial blood varies little from 39 volumes per cent.

Nearly all the carbon dioxide exists in the plasma, where some of it appears to be chemically combined with soda salts.

Nitrogen.—The amount of nitrogen does not vary much, being in both venous and arterial blood about 1·5 volume per cent., and it would appear to be simply absorbed.

For further details about the gases of arterial and venous blood, see Respiration.

CHAPTER XV.

COAGULATION OF THE BLOOD.

In speaking of the chemical relationship of the plasma (see p. 178), the formation of fibrin has been mentioned as the essential item in coagulation, and the relation of fibrin to its probable precursors has been discussed. If the points there explained be borne in mind, and the presence of the corpuscles be taken into account, the various characteristics of the *clot* which forms when blood is shed into a vessel can be easily understood, and should require no further description.

The great importance of the coagulation of the blood in arresting bleeding, and in certain pathological processes, makes it expedient, however, to consider more closely the steps of the process and to enquire into the various circumstances which facilitate its occurrence after the blood is shed, as well as in the living vessels.

Coagulation of Shed Blood.

Before the formation of a perfect clot, blood may be seen to pass through three stages : 1, viscous ; 2, gelatinous ; 3, contraction of clot and separation of serum.

The first stage is commonly very short, and in thin layers of blood passes immediately into the second. In cold weather considerable quantities of blood, if contained in deep vessels, take a much longer time to stiffen, so that the first stage may occupy from one minute to some hours.

The second stage, when the mass has been turned into a firm jelly, may be arrived at within the varying limits just named, and occupies a corresponding period : only a few minutes if the mass be small, spread out or shaken, but many hours if a large quantity be kept motionless and cool.

The third stage therefore begins sometimes as soon as ten to fifteen minutes, but generally after some hours. Clear drops of

serum appear about the clot. After several hours this contracts until it forms but a comparatively small mass floating in the serum. If the jelly-like clot be disturbed, the serous fluid makes its appearance much sooner than the time just stated.

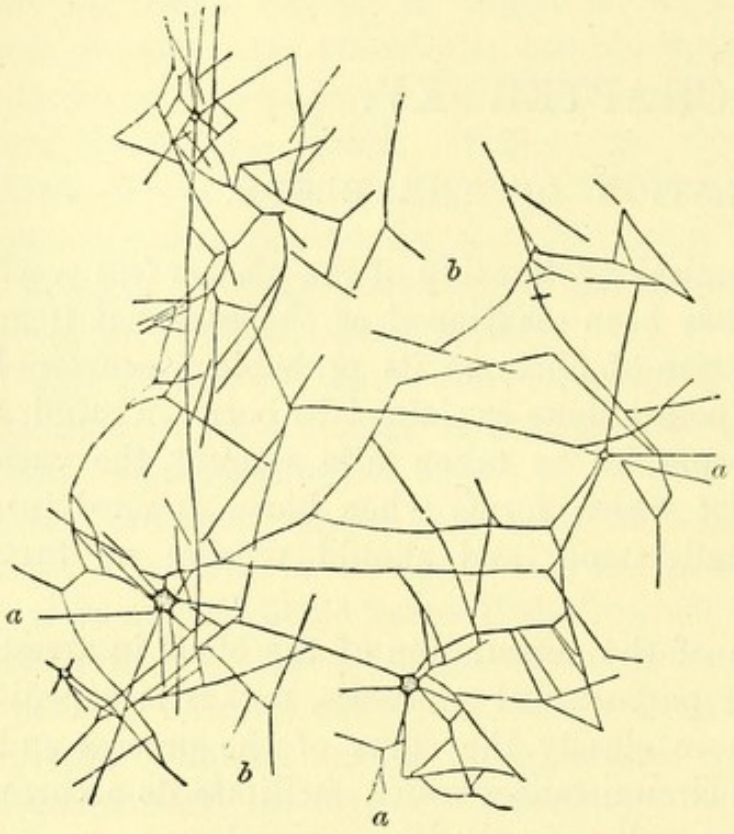


Fig. 109.—Reticulum of Fibrin Threads after staining has made them visible. The network (*b*) appears to start from granular centres (*a*). (Ranvier.)

During the formation of the clot under ordinary circumstances the corpuscles are entangled in the meshwork of fibrin, so that the gelatinous mass has throughout a dark-red colour.

If the coagulation takes place slowly—as it does in very cold weather, in horses' blood, or in human blood if removed from a person during fever—then the heavier red corpuscles have time to subside to the lower layers of the clotting plasma, while the white cells are caught in the meshes of the fibrin and remain in the upper layer of the clot, which then has the pale colour familiar to the physician in the old days of bleeding as the "buffy coat," or *crusta phlogistica*. This buffy coat contains a greater proportion of the elastic fibrin and soft white cells than the rest of the clot, and encloses but few red corpuscles, therefore the fibrin can contract more completely in this upper layer than in the deeper part of the clot which includes the red corpuscles. The effect of this is, that the upper surface becomes concave, and a "cupped" clot is formed. The contraction of the clot proceeds for days, and in order to see the characters described above, the blood should be kept in a cool place and perfectly motionless.

The contraction of the fibrin and separation of the serum can be made to take place much more quickly by gentle agitation causing the ends of the fibrin threads to separate from the sides of the vessel, but

by thus disturbing the clot, during its formation, the corpuscles are displaced and escape into the serum, which is then stained and cannot be seen in its clear transparent state.

If brisk agitation with a glass rod—or better, a bundle of twigs—be commenced the moment the blood is drawn, the fibrin is formed more rapidly, but the corpuscles are not entangled in its meshes, for as quickly as the elastic threads are formed they adhere to and are removed by the rod or twigs. Thus the fibrin is formed very rapidly, and the ordinary stages in the formation of a blood-clot, consisting of fibrin and the corpuscles, do not occur, for the fibrin is separated from the corpuscles as quickly as it is formed. We then have what is commonly spoken of as "defibrinated blood," which does not give a blood-clot. Not that the coagulation has been prevented, but the material essential for the formation of a clot has been removed as quickly as formed, and instead of catching the corpuscles in the meshes of its delicate fibrils to form the clot in the ordinary way, the stringy shreds of fibrin cling around the beating-rod as a jagged mass. The following tables show the relation of the different constituents of coagulated and defibrinated blood respectively :—

$$\text{Living blood} = \left\{\begin{array}{l}\text{Plasma}\\ \text{Corpuscles}\end{array}\right\} = \left\{\begin{array}{l}\text{Serum (appearing as clear fluid).}\\ \left.\begin{array}{l}\text{Fibrin} +\\ \text{Corpuscles}\end{array}\right\} = \text{Blood-clot.}\end{array}\right.$$

$$\text{Living blood} = \left\{\begin{array}{l}\text{Plasma}\\ \text{Corpuscles}\end{array}\right\} = \left\{\begin{array}{l}\text{Fibrin (removed on the rod).}\\ \left.\begin{array}{l}\text{Serum} +\\ \text{Corpuscles}\end{array}\right\} = \begin{array}{l}\text{Defibrinated}\\ \text{blood.}\end{array}\end{array}\right.$$

Many circumstances influence the rapidity with which a blood-clot is formed. Speaking generally, circumstances which tend to injure the corpuscles or the plasma, and give rise to changes resulting in their death, promote coagulation ; while, on the other hand, conditions which protect the corpuscles and impede fibrin formation must retard coagulation.

These may be arranged categorically, viz.

A. Circumstances promoting coagulation :—

1. *Contact with foreign bodies* is of the first importance in hastening coagulation. The greater the surface of contact with the vessel or the air, the more the corpuscles are exposed to injury, and the more rapid are the destructive chemical changes inducing fibrin formation. Thus a drop or two of

blood falling on any surface so as to spread out in a thin layer clots almost instantly.

2. *Motion*, by renewing the points of contact between the blood and the moving agent, hastens coagulation. Thus, by whipping fresh blood, all the fibrin can be removed in a few minutes, and the defibrinated blood left without a clot.
3. *Moderate heat.* The formation of the fibrin generators and the action of the ferment seem to go on more rapidly at 38° —40° C. than any other temperature.
4. *A watery condition of the blood* causes rapid coagulation but a soft clot. This is seen in repeated bleedings or hæmorrhages ; the blood which flows last clots first.
5. The addition of *a small quantity of water*, by setting up rapid changes in the corpuscles, accelerates coagulation.
6. *A supply of oxygen.*—Oxygen is used up in the chemical changes attendant upon the death of the blood, and its presence aids the formation of firm clots, such as are produced in arterial blood. Exposure to the air in a shallow vessel facilitates coagulation, partly by extensive contact and partly by a free supply of oxygen. But exposure to air is not necessary, for blood collected in mercury, without ever coming in contact with the air, coagulates very rapidly.

B. Circumstances which retard coagulation :—

1. Constantly renewed and close inter-relationship with the *lining of healthy blood-vessels* alone affords the requirements essential for the preservation of the living corpuscles and plasma in their normal condition.
2. When the blood is surrounded by *healthy living tissues* interchanges may occur between them, and if the oxygen supply is deficient, coagulation is much delayed. Thus considerable quantities of blood effused into the tissues may remain liquid and black for many days. This dark blood clots on removal and exposure to the air.
3. *Low temperature.*—The rate of coagulation decreases below 38° C., and the process is checked at 0° C.
4. The addition of concentrated *solutions of neutral salts* (about three volumes of 30 per cent. solution of magnesium sulphate) quite prevents coagulation.
5. The introduction of peptone into the blood.
6. An extract of the mouth of the leech has a remarkable power of preventing coagulation.

7. *A great quantity of water* seems to render the action of the fibrin factors weak.
8. The addition of *egg albumin*, *syrup*, or *glycerine*.
9. The addition of *small quantities of alkalies*.
10. The addition of *acetic acid* until very slight acid reaction is obtained.
11. Increase in the amount of *carbon dioxide*. This, together with the want of oxygen, explains why venous blood clots more slowly and loosely than arterial, and why the blood in the distended right side of the heart is frequently liquid after death from suffocation.
12. The blood of persons suffering from inflammatory disease coagulates slowly, but forms a very firm clot, which is "buffed and cupped."

Coagulation within the Vessels.

Since the blood coagulates spontaneously when removed from the body, the question now arises, how does it remain fluid in the blood-vessels?

Though this question has long occupied much attention, it is still difficult to formulate a definite answer. Nor can we expect to find any adequate explanation until we are better acquainted with the exact details of the origin of the fibrin generators. It must be remembered that the blood may be regarded as a tissue, made up of living constituents requiring constant assimilation and elimination for the maintenance of its perfectly normal conditions and life. We can confidently say that coagulation is the outcome of certain chemical changes concomitant with the death of the blood, and that while it lives no such changes take place. But such an answer adds little to our knowledge of the matter.

Since constant chemical intercourse must be kept up between the blood and its surroundings in order to sustain the complex chemical integrity essential for its life, we cannot be surprised that its waste materials accumulate, and that it soon dies when shed, as other tissues do when deprived of their means of support. The formation of a solid and the separation of a liquid form of proteid is in no way unusual as a first step in the decline from exalted chemical construction, for similar changes occur in other tissues, and in protoplasm itself. The soft contractile substance of muscle probably tends during its contraction, and certainly at its death does undergo almost exactly the same kind of change as the blood in coagulation.

If we knew accurately the nutritive process taking place in the blood itself, and with which of its surroundings it keeps up chemical interchange, the answer would be much simplified. But we have in the blood three elements that probably have different modes of assimilation and elimination, viz., plasma, white cells, and red discs. We practically know nothing of the changes they undergo during their nutrition; or whether their tissue changes have a necessary relation to those of the neighbouring tissues. We do know, however, that there exists some very intimate relation between the membrane lining the vessel walls and the contained blood. They seem to require frequently repeated contact one with the other in order that the normal condition of both may be maintained in perfect vital integrity. That fresh supplies of blood are required by the vessel wall, may be shown by the fact that when deprived of its nutriment by a stoppage of the blood-flow, it soon loses its power of retaining the blood, and admits of extravasation. And that renewed contact with the vessel wall is equally necessary for the integrity of the blood, is seen from the fact that the cells congregate, the discs adhere together, and the plasma coagulates when stasis interferes with its intercourse with fresh parts of the intima. Probably the chemical changes going on in the one are useful for the nutrition of the other, and they mutually supply one another with some material essential for their life. This is apparent in those cases where coagulation takes place during life in the vessels. It never occurs so long as the intima of the vessel is perfect, and the blood-flow constant, but it follows lesion of this delicate membrane, whether caused by injury or mal-nutrition.

The gradual occurrence of this impairment of function of the intima can be watched under the microscope in the small vessels of a transparent part during the initial stages of inflammation. Owing to the arrest of the flow of blood, the walls of the small vessels suffer from defective nutrition, and may be seen to allow some elements to escape, while the discs adhere together and the plasma coagulates.

In the larger vessels the same thing occurs when inflammation of their lining membrane destroys its capability of keeping up the necessary nutritive equilibrium. Thus clots form on the inner lining to the walls of an inflamed vein, often growing so as to fill the entire vessel, and give rise to a condition called *thrombosis*.

On the valves of the left side of the heart and in the arteries where the delicate intima is subjected to great mechanical strain, it is common enough to find slight injuries of it covered over with thin clots. To the surgeon this mutual nutrition of intima and blood is

of the utmost importance in attaining the occlusion of vessels, for it is upon this fact he has mainly to depend for the stoppage of hæmorrhage from a wounded artery. A tightly-tied ligature either injures the inner coats mechanically, or starves the intima by checking the flow of blood through the vessel up to the next branch, and that portion of the vessel is filled with stationary blood, which soon clots and forms an adherent plug. But if the ligature be applied too loosely, a slight blood current passes through the point where the vessel is tied, and this suffices for the nutrition of the intima by the renewal of the blood's contact, so that no clot is formed, the vessel is not closed, and most probably when the ligature has cut through the outer coat, "secondary hæmorrhage" occurs.

It has also been shown that if any foreign substance, such as a thread, be introduced into the blood while circulating, a coagulum will form around it. From this it would appear that the presence of a substance which cannot carry on the necessary chemical intercourse with the blood will excite irritation in its elements, and so effect slight local death of the plasma and the production of fibrin.

The time required for the production of intravascular coagulation as a result of mere stasis is happily long, for it has been found that the blood current may be stopped in a limb, by pressure or otherwise, for many hours without coagulation occurring. Indeed, cases have occurred where a tight bandage has stopped the circulation for an entire day without injurious consequences. This is explained by the fact that so long as the intima lives, the blood remains fluid; in short, the tissues die before the blood clots in the vessels.

The tissues continue to live for some time after the animal is dead, and so we see the blood remains fluid in the vessels a considerable time, in fact, as long as the vessel wall can nourish itself and live. Thus it has been shown that the blood in a horse's jugular vein separated by ligature from the circulation, and removed from the animal, will remain fluid for fully twenty-four hours.

In cold-blooded animals the tissues live for even a longer time. The heart of the tortoise, if kept under suitable conditions, will beat for two days when removed from the body, and as Brücke has shown, blood contained in it will remain fluid until after the heart is dead.

If the details of the fibrin formation within the blood-vessels be followed, it is found that the injured spot or foreign body first becomes covered over with white corpuscles, around which threads of fibrin appear attached to the rough surface. As more fibrin is

formed and the layer thickens, only a few cells can be seen in its meshes, but a great number always exist on the surface of the new fibrin, forming a layer between it and the blood. It is further remarked that coagulation has some relation to the abundance of white cells in all spontaneously coagulated fluids. The more cells, the firmer the clot. In pathological exudations also, and those acute serous collections which coagulate on removal from the body, fine granular threads of fibrin seem to start from the white cells, and radiate from them in a stellate manner. (Figs. 100 and 109.)

When white cells congregate at a point of a vessel from which the intima is stripped, their more active exertion possibly produces the ferment, &c. And at the same time they remain at the injured part of the vessel wall, and the removal of the fibrin factors cannot occur at the place of injury, since the intima is destroyed. Thus, local clots are formed which extend over the injured surface, and by a process of organisation, the repair of the denuded patch is accomplished.

Some believe that a great number of white blood-cells undergo chemical disintegration the instant the blood is shed, and consider that the fibrin ferment, and probably other fibrin generators, are the result of the destruction of these weak cells, and exclude the red corpuscles from taking any share in the process.

There is some evidence, however, that the plasma and the discs can give rise to all the fibrin factors, and we know that in the circulation white cells must be destroyed and yet cause no coagulation.

If some fresh blood be allowed to flow into a fine capillary tube, the white cells can be seen to move away from the red discs, and the formation of the clot—a delicate fibrin network enclosing the discs—may be watched. Here some at least of the white cells exhibit manifestations of life for a considerable time after the clot has been formed, and their death could not have been the source of the fibrin factors.

In conclusion, then, we can only suppose that, as in other tissues, some chemical changes must go on in the elements of the blood in order to preserve its integrity. A cessation of these changes gives rise to new products which produce fibrin, and hence cause coagulation. But so long as the elements of the blood are frequently brought into close relationship with a healthy vessel wall, the fibrin factors are either produced in such small quantity as to be ineffectual, or they are altered, destroyed, or taken up by the intima and possibly utilised for its nutrition. When the blood is removed from the vessels, the production of the fibrin factors proceeds effectually,

either on account of the blood elements undergoing destructive changes, the products of which accumulate ; or owing to the impossibility of re-integration, the fibrin factors appear as a product of lethal chemical change or decomposition.

In accepting the first view, we only adopt the theory of John Hunter, who thought coagulation was an act of life. If we adopt the other view, we must needs say it is an act of death. But, after all, this is a mere difference in degree, for how can we distinguish between the unsuccessful attempt of a living tissue to re-integrate, or regain the chemical properties upon which its life depends, and the inevitable result of failure, which, if prolonged beyond a certain point, must cause its death ?

CHAPTER XVI.

THE HEART.

THE course taken by the blood on its way to the various parts of the body is called the *circulation*, on account of its having to make repeatedly the circuit of vessels leading to and from the heart. The heart is the great motor power which drives the blood through all the vessels, of which there is one set belonging to the circulation of the organs of the system generally, and another leading to and from the lungs.

Anatomists speak of two circulations—the greater or *systemic*, and the lesser or *pulmonary*. However, if we follow the course of the blood, we see that both these sets of vessels really belong to the one circulation, and in fact form but one circuit. In all the higher animals the heart forms a single organ, but it really is composed of two muscular pumps which are anatomically united though distinct in function. These functionally distinct hearts work at different parts of the circuit traversed by the blood. The blood on its way through the lungs and systemic vessels visits the heart twice, in order to acquire the force necessary to overcome the resistance of these two sets of vessels. The right heart is visited before the pulmonary vessels, and is the agent for pumping the blood through the lungs. The left heart is placed before the systemic vessels and pumps the blood through the body generally. Thus anatomically there appear to be two circulations and but one heart; physiologically there is one circulation and two hearts; or two separate points of resistance and a distinct pumping organ to drive the blood through each.

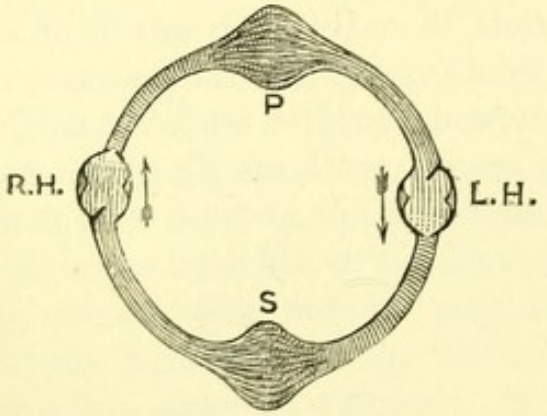


Fig. 110.—Diagram of Circulation, showing right (R.H.) and left (L.H.) hearts, and the pulmonary (P) and systemic (S) sets of capillary vessels.

The circulation might then be represented by a simple diagram (Fig. 110) in which the direction of the current is indicated by the arrows. L. H. shows the position of the left or systemic pump, and S. the resistance in the systemic vessels. R. H. represents the pulmonary pump and P. the second obstacle in the circuit, viz., the vessels of the lungs. This functional distinction must be kept in view in studying the dynamics of the circulation, although the two pumping organs are fused into one viscus, with two distinct and separate channels for the passage of the blood.

In each system of blood vessels we have the same general arrangement for the distribution and re-collection of the blood.

In passing from either the right or left side of the heart the blood flows into tubes called arteries, which divide and subdivide until the branches become microscopical in size. From the very minute arteries the blood passes into the *capillaries*, which cannot be said to branch, but form a network of delicate tubes with meshes of varying closeness according to the tissue.

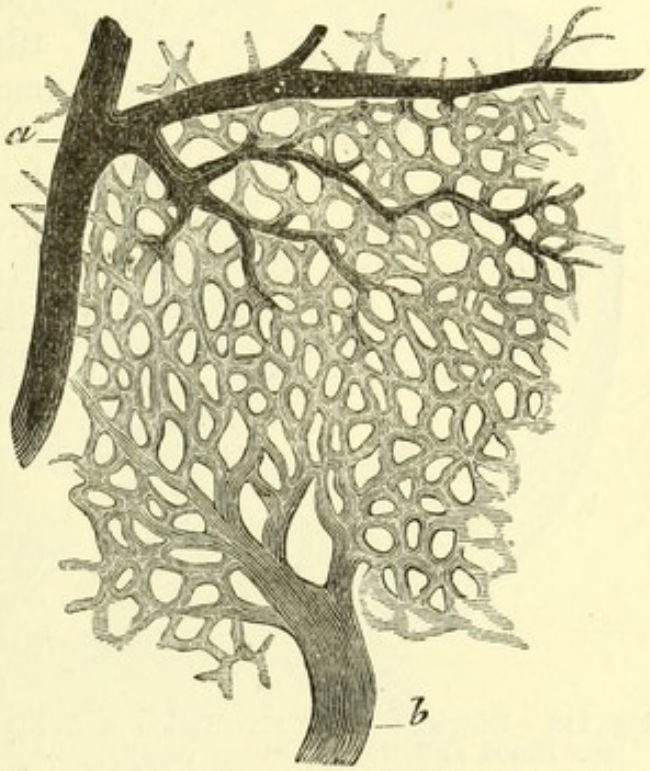


Fig. 111.—Capillary Network of the Choroid of Child of a few months old. (Cadiat.)
(*a*) Artery. (*b*) Vein, and capillary network intervening.

Connected with the meshes of the capillaries are the small veinlets which collect the blood from the networks (Fig. 111). These unite, gradually forming larger vessels, which again are but the tributaries of the large veins which convey the blood back to the heart.

About three hundred years ago the true course of the blood current through the systemic and pulmonary heart, arteries and veins, so as to form one circle, was demonstrated by Harvey. Before his time only the so-called "lesser" or pulmonary circuit was known. The magnifying glasses at his disposal did not enable him to see the capillaries, which were first described by Malpighi some fifty years later.

In the hope of making their different functions appear more

striking, the various parts of the circulatory apparatus may be enumerated as follows, and roughly illustrated by a diagram :—

1. The left (systemic) heart (L. H.) pumps the blood into the systemic arteries, and thus keeps these vessels over-filled.

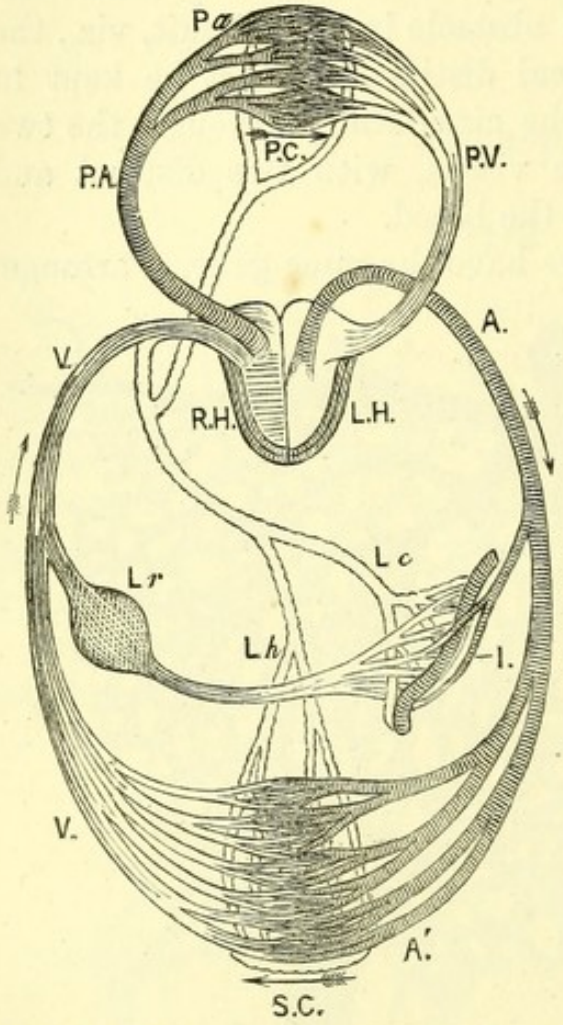


Fig. 112.—Diagram of the Circulation of the Blood and the absorbent vessels. For details see text.

2. The larger systemic arteries (A.), by their elasticity, exert continuous pressure on the blood with which they are distended.

3. The smaller systemic arterioles (A'.), by their vital contractility, check and regulate the amount of blood flowing out of the larger arteries into the capillaries, and thus keep up a high pressure in the larger arteries.

4. In the systemic capillaries (S. C.), the essential operations of the blood are carried out, viz., the chemical interchanges between it and the tissues.

5. The wide systemic veins (V.), are the passive channels conveying the impure blood to the pulmonary heart.

6. The right (pulmonary) heart (R.H.), pumps the blood into the pulmonary arteries and distends them.

7. The pulmonary arteries (P.A.), press steadily upon the blood and force it through :—

8. The small pulmonary arterioles (P.*a*.), regulate the flow into the capillaries of the lungs.

9. In the pulmonary capillaries (P.C.), the blood is exposed to the air, and undergoes active gas-interchange.

10. The pulmonary veins (P. V.) carry the blood to the left heart, and thus complete the circuit.

Lh. indicates the lymphatics, which drain the tissues, and Lc. the lacteals, which absorb from the stomach and intestines (I.)

Although the blood enters the arteries by jerks, its motion through the capillaries is even, because the arteries constantly press on the blood they contain, their elastic walls being distended by the pump-

ing of the heart, which fills the aorta and arteries more quickly than they can empty themselves, unless the adequate pressure has been attained. The contracting arterioles are the chief agents in resisting the outflow, and keeping up the arterial pressure.

The Heart.

The heart of man and other warm-blooded animals may be said to be made up of two muscular sacs, the pulmonary and systemic pumps,

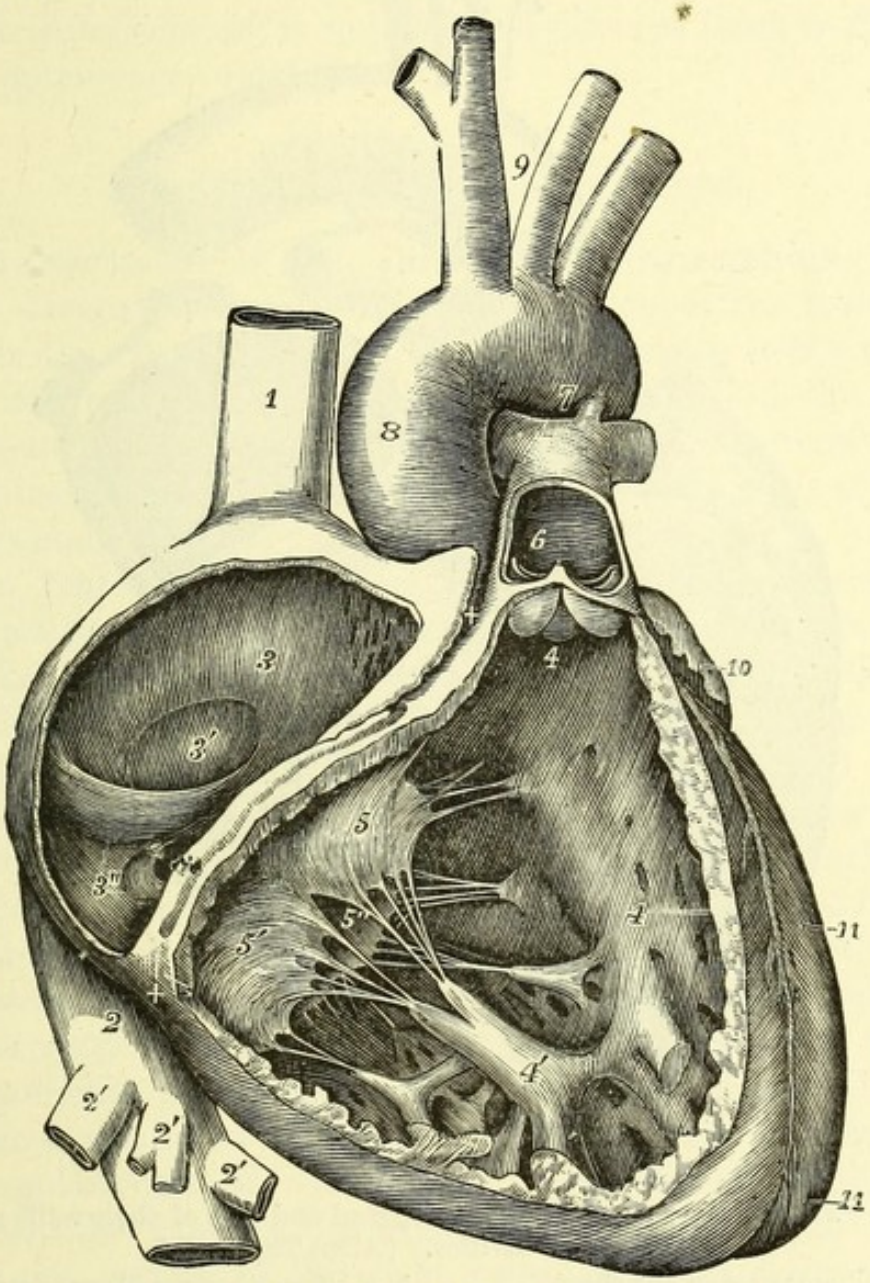


Fig. 113.—Interior of Right Auricle and Ventricle exposed by the removal of a part of their walls. (Allen Thomson.)

1. Superior vena cava.
2. Inferior vena cava.
2′. Hepatic veins.
3, 3′, 3″. Inner wall of right auricle.
4, 4. Cavity of right ventricle.
4′. Papillary muscle.
5, 5′, 5″. Flaps of tricuspid valve.
6. Pulmonary artery, in the wall of which a window has been cut.
7. On aorta near the ductus arteriosus.
8, 9. Aorta and its branches.
10, 11. Left auricle and ventricle.

or, as they are commonly termed, the right and left sides of the heart; between these no communication exists after birth. Each of these sacs may be divided into two chambers: one, acting as an ante-chamber, receives the blood from the veins; it has very thin walls

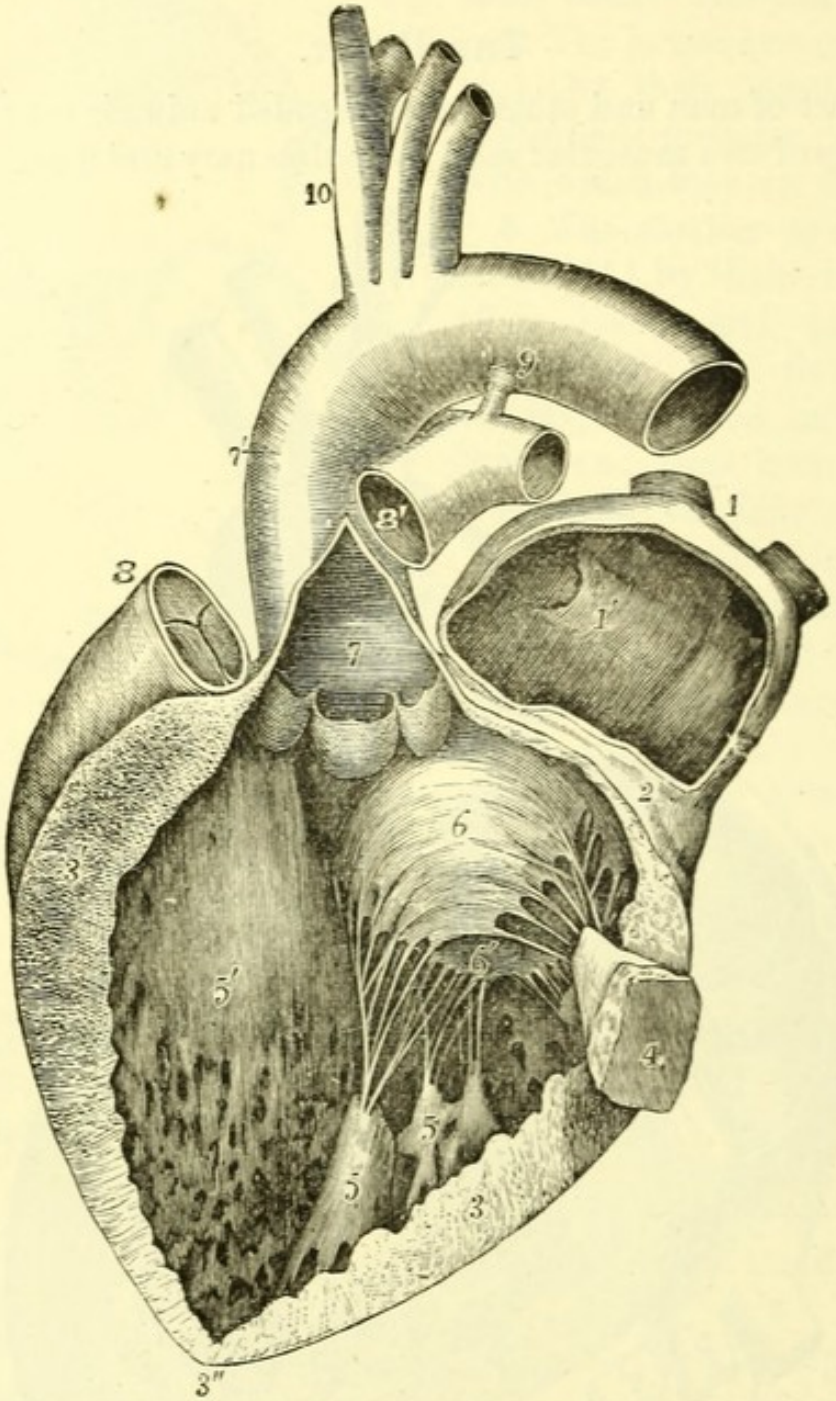


Fig. 114.—The left Auricle and Ventricle opened and part of their walls removed to show their cavities. (Allen Thomson.)

1. Right pulmonary vein cut short.
1′. Cavity of left auricle.
3. Thick wall of left ventricle.
4. Portion of the same with papillary muscle attached.
5, 5′. The other papillary muscles.
6. One segment of the mitral valve.
7. In aorta is placed over the semilunar valves.

and is called the *auricle*; the other, the *ventricle*, is the powerful muscular chamber which pumps the blood into and distends the arteries. (Figs. 113 and 114.)

In the empty heart the great mass of the organ, which forms a blunted cone, is made up of the ventricles, while the flaccid auricles are found retracted to an insignificant size at its base. The four cavities have the same capacity, namely, about six ounces or eight cubic inches when distended.

The walls of both the auricles are about the same thickness, while the amount of muscle in the walls of the ventricles differs materially. The wall of the left ventricle, including that part which forms the interventricular septum, is nearly three times as thick as that of the right or pulmonary ventricle.

Arrangement of Muscle Fibres.

At the attachment of each auricle to its corresponding ventricle there is situated a dense ring of tough connective tissue, which surrounds the openings leading from the auricles to the ventricles. Similar tendinous rings (zona tendinosa) exist around the orifice of the aorta and pulmonary arteries. These tendinous rings form the basis of attachment for the muscle bundles of the walls of both the ventricles and auricles.

In the ventricles many layers of muscles can be made out. The outer fibres pass in a twisted manner from the base towards the apex, where they are tucked in so as to reach the inner surface of the ventricular cavity. They then pass back to be attached at the base; some passing into the papillary muscles are connected with the cardiac valves through the medium of the chordæ tendineæ; and the others forming irregular masses of muscle on the inner surface of the cavity, pass in various directions towards the base, to be fused with the tendinous rings around the arterial orifices. Another set of layers passes transversely around the ventricle lying between the inner and outer sets, and passing nearly at right angles to them.

The muscular fibres forming the thin auricular walls have their origin from the zones of the auriculo-ventricular orifices, and pass very irregularly around the cavities. The outer set of fibres have a transverse, the inner a longitudinal direction. Bands of fibres encircle the orifices of the great veins, and extend for some little distance along the vessels, particularly on the pulmonary veins, which have thick circular muscular coats after they leave the lungs.

The fibres of the auricles are not directly continuous with those of the ventricles, the auricular and ventricular fibres being only related to each other by their points of origin, viz., the auriculo-ventricular fibrous zones.

Minute Structure.

The muscle tissue of the heart differs both in structure and mode of action from the other contractile tissues of the body. The elements are firmly united with one another to form irregular close networks, which, however, can be broken up into masses easily recognisable as peculiar cells. These cells are irregular prismoidal blocks, the blunt ends of which are often split, allowing connection with two contiguous cells. They contain a nucleus, situated in the central axis of the cell. The cells are not surrounded by a distinct sheath of sarcolemma.

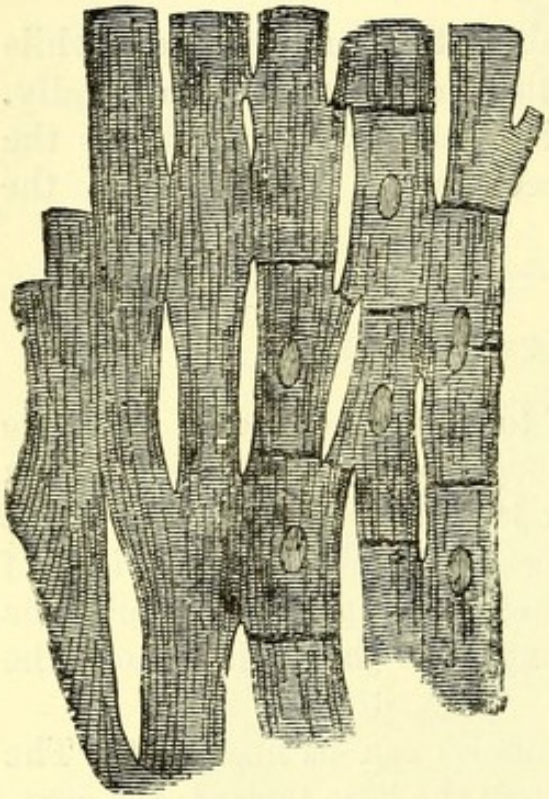


Fig. 115.—Striated Muscle Tissue of the Heart, showing the trellis-work formed by the short branching cells, with central nuclei.

Though striated the action of the heart muscle is peculiarly independent of the higher nervous centres, being quite involuntary; it is characterised by a definite periodicity and is incapable of tetanus. The duration of its contraction is very long when compared with that of the skeletal muscles, but is much shorter than that of the contracting tissues of most hollow viscera.

Valves.

The orifices which lead into and out of the ventricles have peculiar arrangements of their lining texture, forming valves which allow the blood to pass only in a certain direction. These valves, which form a most interesting and important part of the economy of the heart, are of two kinds, each differing in their mode of action. One prevents the passage of the blood from the ventricles to the auricles, the other guards the openings into the great arteries.

The *auriculo-ventricular valves* have a sail-like action. They are made up of delicate curtains formed of thin sheets of connective tissue arising from the margins of the auriculo-ventricular openings which form the fixed attachment of each of the curtains of the valves. The free edges and ventricular surfaces of the curtains are blended

with the tendinous cords coming from the papillary muscles, and thus give points of tendinous attachment to some of the bundles of muscle fibres in the wall of the ventricle. At the right auriculo-ventricular opening there are three chief curtains; hence it is called

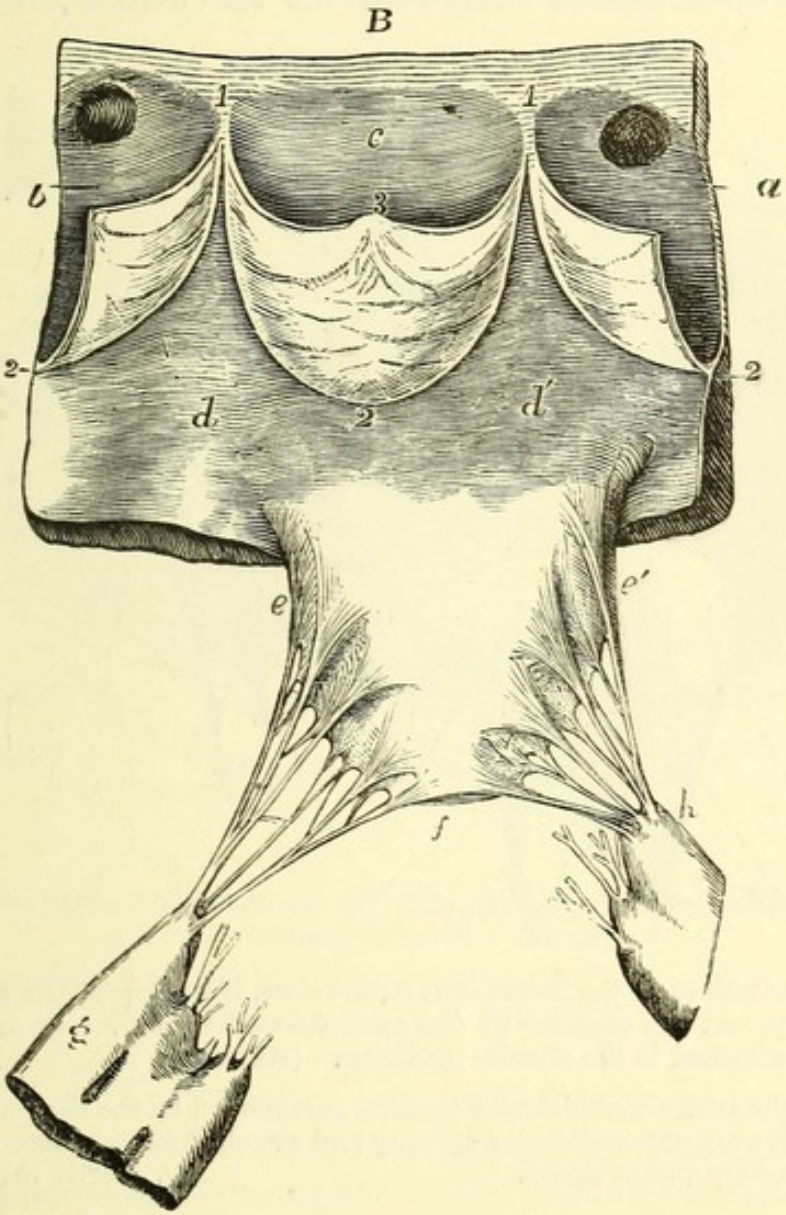


Fig. 116.—Portion of the Wall of Ventricle (*d d'*) and Aorta (*a b c*), showing attachments of one flap of mitral and the aortic valves; (*h* and *g*) papillary muscles; (*e*, *e*, and *f*) attachment of the tendinous cords. (Allen Thomson.)

the "tricuspid" valve (Fig. 117, *RAV*). The opening from the left auricle to the left ventricle, which is about one-third smaller, is guarded by two large valvular flaps, and is hence called the "bicuspid," or more commonly "mitral" valve (Fig. 116).

The *aortic* and *pulmonary valves* are made up of three deep *semi-lunar pockets* with free margins looking towards the vessel. The convex base of each pocket is attached to the arterial orifice of the ventricle, with the lining membrane of which it is continuous.

Action of the Valves.

Auriculo-ventricular Valves.—The mode of action of the flaps of the tricuspid and mitral valves is like that of a lateen sail of a boat, if we substitute the blood stream for the air current; the tendinous

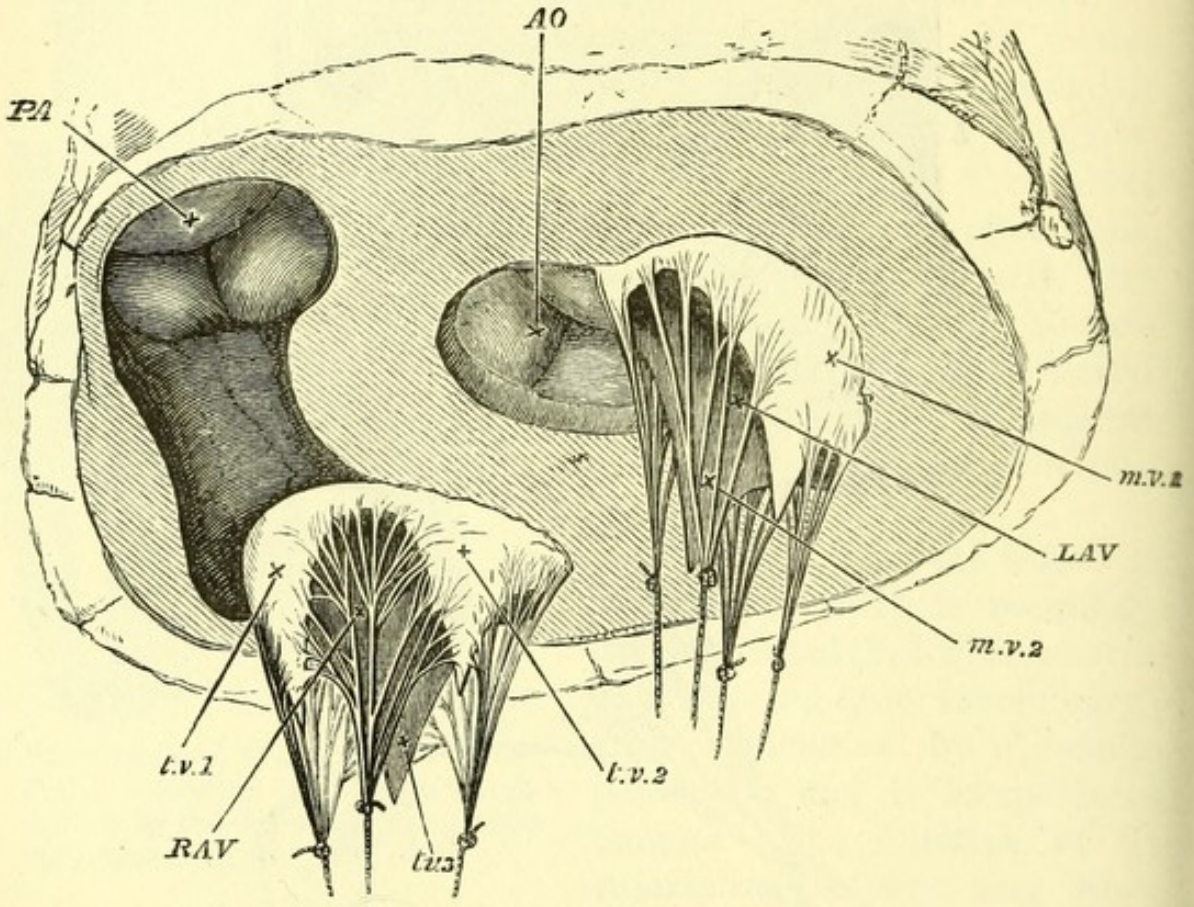


Fig. 117.—The Orifices of the Heart seen from below, the whole of the ventricles being cut away, and the curtains of the auriculo-ventricular valves drawn down by threads attached to the chordæ tendineæ. (Huxley.)

RAV. Right auriculo-ventricular opening surrounded by the flaps of tricuspid.
LAV. Left auriculo-ventricular opening and attached mitral valve.
PA. Pulmonary valves closed. *AO.* Aortic valves closed.

cords acting as the "sheet" or rope which restrains the sail when filled with wind.

The curtains of the valves may at first be considered as lying close to the ventricular wall. As the ventricle gradually becomes filled, the flaccid muscular wall is moved away from the valves, which are held in the midst of the fluid by the tendinous cords coming from the elastic papillary muscles. When the auricle contracts, a column of blood is driven into the ventricle, which, though not distended, is already filling with blood. This sudden central inflow gives rise to lateral back-eddies, which get behind the flaps of the valves and carry them towards the auricle. By the time the auricle has emptied itself

into the ventricle, the flaps of the valves are in contact with each other and the orifice is closed. When the ventricle begins to contract upon its contained blood, the pressure makes the valves tense and the fluid bellies out the sail-like flaps towards the auricles, so that their convex sides come into still closer apposition with one

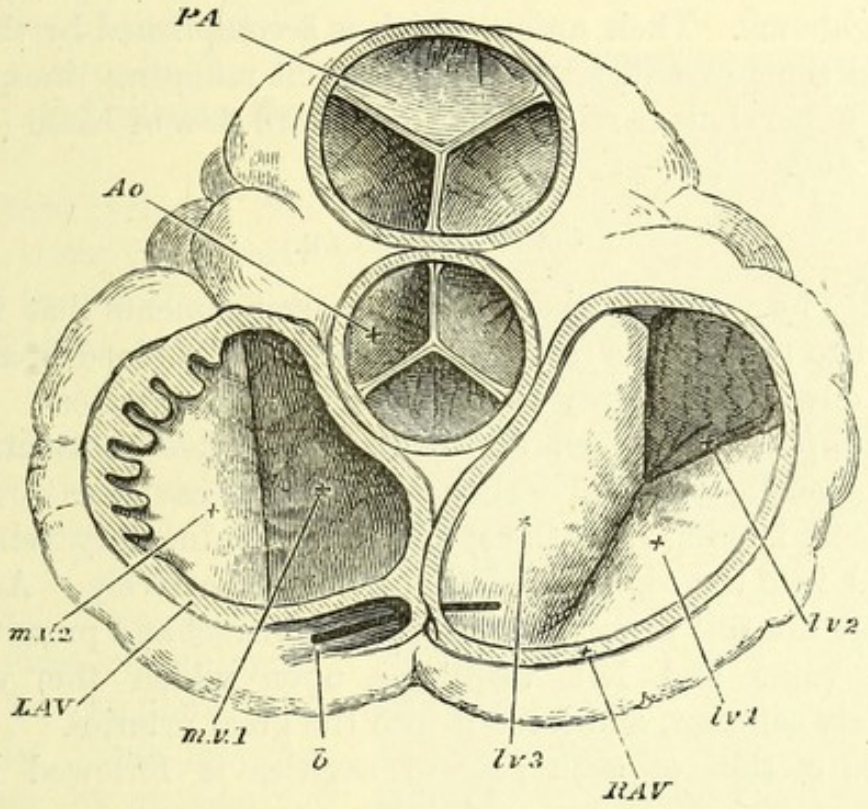


Fig. 118.—The Orifices of the Heart seen from above, both the auricles and the great vessels being removed. (Huxley.)

PA. Pulmonary artery and its semilunar valves. *Ao*. Aorta and its valves. *RAV*. Tricuspid, and *LAV*. Bicuspid valves.

another. Their free margins are held firmly in position by the papillary muscles contracting and tightening the cords. The flaps are kept at much the same tension by the papillary muscles shortening in proportion as the ventricle empties itself and the cavity diminishes in size. By this mechanism the valves are prevented from bulging too much into the auricles, or allowing the blood to pass back into them.

THE ARTERIAL VALVES :—The *semilunar valves* are mere membranous pockets, and have no tendinous cords attached to them ; but on account of the extent of their convex attachment, when their free margin is made tense by the pocket being filled from the artery, the valves can only pass a given distance from the wall of the vessel and are thus held firmly in position. The force of the blood leaving the ventricle distends the vessel and pushes its wall away from the less

elastic valve. When the force begins to diminish, the blood passes behind the semilunar flaps and raises them from the wall of the distended artery. The moment the current from the ventricle has ceased to flow, the pockets are forced back by the aortic blood pressure and bulge into the lumen of the vessel, so that the convex surface of the lunated portions of each valve is pressed against corresponding parts of its neighbours. Their union, which is accomplished by their overlapping to some extent, forms three straight radiating lines, and is a perfectly impervious barrier to any backward flow of blood (Fig. 118, *PA.* and *Ao.*).

Cardiac Cycle.

It is only by means of these valvular arrangements that the heart is enabled to perform its function of pumping the blood in a constant direction onwards to empty the veins and fill the arteries.

This pumping is carried on by the successive contractions and relaxations of the muscular walls of the various cavities.

The blood, flowing from the systemic and pulmonary veins, passes unopposed into the right and left auricles respectively. As soon as the auricles are full their walls suddenly contract and press the blood into the right and left ventricles, upon which the ventricles immediately contract, and force it into the great arteries.

The contraction of each pair of cavities is followed by their relaxation.

The blood cannot pass back into the veins from the auricles when they contract, because the auricular contraction commences in the bundles of muscular fibre which surround the orifices of the great venous trunks; and it cannot flow back to the auricles, because, as has been seen, the force of the blood current on its entry into the ventricles, closes the valves; while a backward flow from the large arteries is at once prevented by the current distending the semilunar pockets, and thus firmly closing the valves.

When viewed for the first time, the beat of the heart appears to be a single act, so rapidly does the ventricular follow the auricular beat. More careful examination shows that this single action is composed of different phases of activity and repose, which together make up the *cycle of the heart-beat.* The contraction of the cavities of the heart is called their *systole,* the period of rest is called their *diastole.*

Systole of the Heart.—The systole of the corresponding cavities of both sides of the heart is exactly synchronous; that is to say, the two auricles contract simultaneously, and the contraction of the two ventricles follows immediately that of the auricles.

The ventricular systole follows that of the auricle so closely that no interval can be appreciated. The rapidly succeeding acts of auricular and ventricular systole are followed by a period during which both auricles and ventricles are in diastole, which is commonly spoken of as the *passive interval or pause.*

While the auricles are contracting the ventricles are relaxed, and the relaxation of the auricles commences immediately the ventricular contraction begins.

The entire cycle of the heart-beat, occupying nearly a second in the healthy adult, may be divided into three stages :—

Auricular systole.
Ventricular systole.
General Diastole.

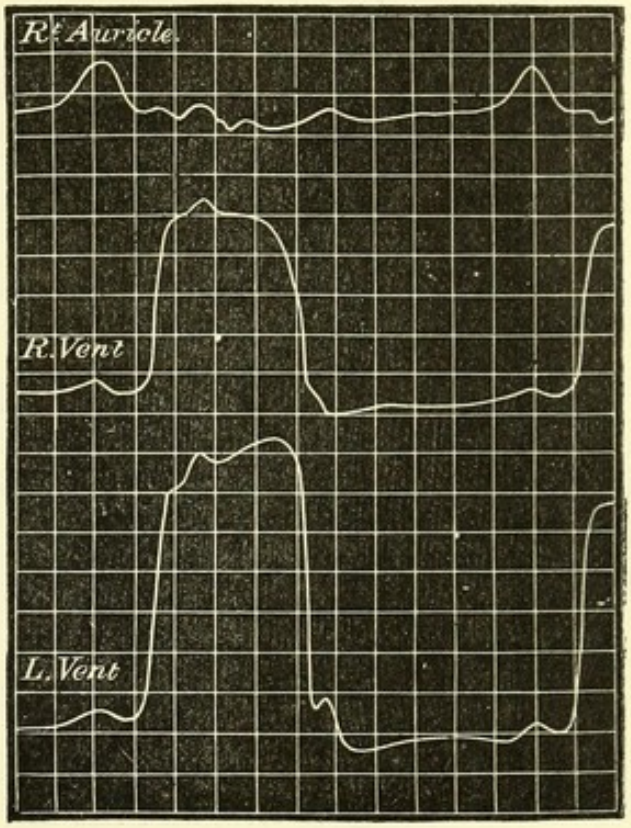


Fig. 119.—Curves drawn on a moving surface by three levers, which are connected with the interior of the heart, viz. :—

Upper line shows the changes of pressure occurring in the right auricle ;
Centre line shows the pressure changes within the right ventricle ;
Lower line shows the changes of pressure occurring in the left ventricle.
(The smoked surface is moved from right to left.) (After Chauvian.)

The exact time occupied by each phase of the cycle can only be calculated approximately. This may be done either by registering graphically the motions of the auricles and ventricles directly communicated to levers brought into contact with their surface, or by recording graphically the pressure changes which occur within the cavities, by introducing into them little elastic sacks filled with air, whence the pressure changes are communicated to an ordinary "tambour," and registered on a smoked surface.

Of the whole period of the cycle the passive interval or pause is the longest and the most variable, for in the ordinary changes in the heart's rhythm the pause alone varies. Next in duration is the ventricular systole, while the shortest is the auricular systole.

The following figures give approximately the proportion of time

occupied by each part of the cycle in the case of a horse, whose intracardiac tension was registered in the manner just referred to while his heart beat about fifty times in the minute :—

	Proportion of cycle.		Duration in seconds.
Auricular systole	$\frac{1}{6}$	=	0·2″
Ventricular systole	$\frac{2}{6}$	=	0·4″
Passive interval	$\frac{3}{6}$	=	0·6″

Or if we assume the human heart to beat some seventy times a minute, each cycle would occupy about $\frac{8}{10}$ of a second, made up as follows :—

Auricular systole	= $\frac{1}{10}$	of a second
Ventricular systole	= $\frac{3}{10}$	,,
Pause	= $\frac{4}{10}$	,,

The duration of the auricular and ventricular systole varies little except under abnormal circumstances, but the pause is constantly undergoing slight changes. In fact, the duration of the general diastole depends upon the rate of the heart-beat, being less in proportion as the heart beats more quickly.

Cardiac Movements.

If the thorax of a recently killed frog be opened, the heart can be observed beating *in situ*, and the different acts in the cycle studied without difficulty.

In mammalians, in order to see the heart in operation, it is necessary to keep up artificial respiration, during which the heart continues to beat regularly, though the thorax be opened. A careful inspection of the beating heart shows that during its cycle of action certain changes take place in the shape and relative position of its cavities. This is owing partly to the change in the amount of their blood contents and partly to the form assumed by the muscular wall when contracting.

During the passive interval the auricles are seen to swell gradually on account of the blood flowing into them from the veins : when the auricular cavities are nearly full, a contraction, commencing in the great venous trunks near the heart, passes with increasing force over the auricles and gives rise to their rapid systolic spasm. The auricles suddenly diminish in size, and appear to become pale. When the blood is being propelled through the auriculo-ventricular openings, the flaccid walls of the ventricles appear to be drawn over

the liquid mass by the contraction of the muscular walls of the auricles (just as a stocking is drawn over the foot by the hands), and the base of the ventricles is thus drawn upwards. The moment the ventricles have received their full charge of blood from the auricles they contract, becoming *shorter* by the movement of the base towards the apex, and *thicker* by their elongated cone becoming rounder. The great arteries are at the same time distended with the blood from the ventricle and elongated, their elastic walls being drawn down over the liquid wedge. The soft elastic tissues are thus in turn made to slide, as it were, over the incompressible fluid that forms the fulcrum, which the muscular walls use as a purchase.

During the systole, when the thorax is open, the ventricles rotate slightly on their long axis, so that the left comes a little forwards, and the apex also forwards and towards the right. When the systole of the ventricles ceases, they become flaccid and flattened, and the gradual refilling of the cavities begins, as there is nothing to prevent the blood flowing from the veins through the auricles into the ventricles, where the pressure, as in all parts of the thorax, is negative. The semilunar valves being closed, the large arteries grasp firmly the blood, and by their steady resilient pressure force it on towards the distal vessels. During this pause the arteries seem to become shorter and to draw the base of the heart up again by lengthening the flaccid ventricles.

The part of the heart which changes its position most is the line between the auricles and ventricles, while the apex remains fixed in one position, only making a very slight lateral and forward motion, which probably does not take place within the thorax. If a thin needle with a straw attached be made to enter the apex through the wall of the chest, the straw does not move in any definite direction during the systole, but simply shakes. If, on the other hand, the needle be placed in the base of the ventricles, the straw moves up and down with each systole and diastole.

Heart's Impulse.

The heart communicates its motion to the chest-wall, and the movement can be felt and seen over a limited area, which varies with the thinness of the individual. This *cardiac impulse*, as the stroke is called, can best be felt in the fifth intercostal space, a little to the median side of the left nipple. It is found to be synchronous with the ventricular systole. During this period—ventricular systole—the base of the ventricles moves downwards and becomes thicker.

The flaccid cone which is formed by ventricles during diastole, is somewhat flattened against the chest-wall, but during systole it becomes rounded and bulges forwards, pushing the chest-wall before it. This change in shape is the chief cause of the cardiac impulse.

If the ventricles be gently held between the fingers during their systole, a most striking sensation is given by the change of shape and the sudden hardening of the muscle. The mass in the ventricles, from being quite soft and compressible during diastole, suddenly acquires a wooden hardness owing to the tightness with which the muscle grasps the fluid, and the greater firmness of the contracting tissue.

This hardening gives the sensation of a sudden enlargement. No matter on what surface the finger be placed, the heart seems to give

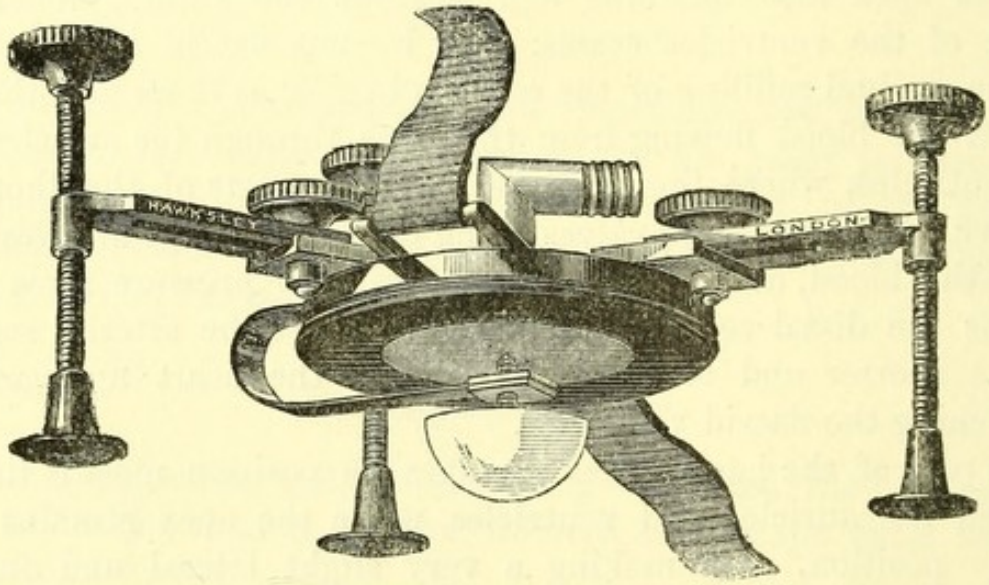


Fig. 120.—Cardiac Tambour, which can be strapped on to chest-wall, so that the central button lies over the heart-beat, and the pressure may be regulated by the screws at the side. To the tube bent at right angles is attached the rubber tube which connects the air cavity with that of the writing tambour shown in Fig. 119.

a slight knock in that direction. Thus, when grasped between the forefinger placed below the diaphragm and the thumb on the antero-superior aspect, the impulse is equally felt by each digit.

The important items in causing the impulse are then, the change in shape of the ventricles from a flattened to a rounded cone, and their simultaneous hardening, which no doubt helps to make the movement more distinctly felt through the wall of the chest.

The point at which the impulse is best felt corresponds to the anterior surface of the ventricles at a considerable distance above the apex; it is therefore erroneous to call the impulse the "apex beat."

The cardiac impulse is a valuable measure of the strength of the systole, and hence is of great importance to the clinical physician. It

may be registered by means of an instrument called the Cardiograph. Many such instruments have been devised, most of which work on the same principle, and make a record on a moving surface with a lever attached to a *tambour*, to which the movements of the chest wall are transmitted from a somewhat similar drum by means of air tubes. In using this plan, so generally employed by Marey, one air tambour (Fig. 120) is applied over the heart, the motions of which cause a variation in the tension of the air it contains; these variations are transmitted by a tube *f*, (Fig. 121) to the other tambour (*b*), where they give rise to a motion in its flexible surface to which a delicate lever is attached at (*a*).

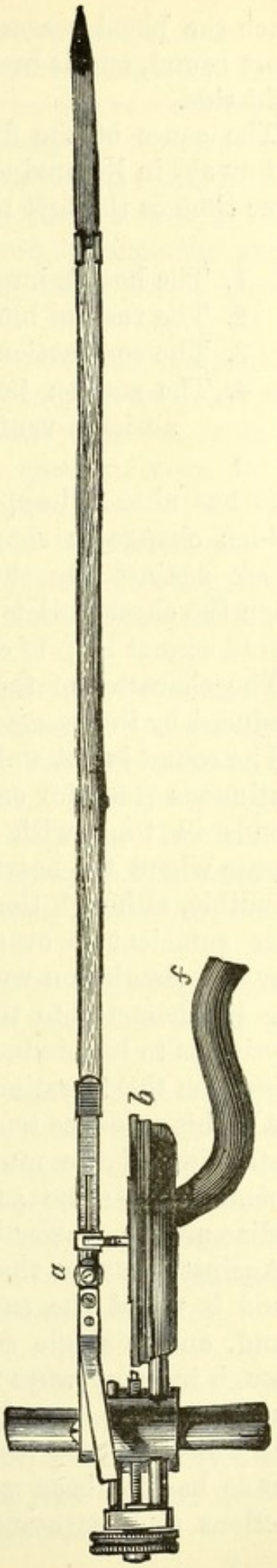


Fig. 121.—Writing Lever and Tambour. (*a*) Joint of the lever; (*b*) Air chamber; (*f*) Rubber tubing connecting it with cardiac tambour.

Heart-Sounds.

The heart's action is accompanied by two distinct sounds, which can be heard by bringing the ear into firm direct contact with the precordial region, or indirectly by the use of the stethoscope.*

One sound follows the other quickly, and then comes a short pause; consequently they are spoken of as the *first* and *second* sounds.

The first sound is heard at the beginning of the ventricular systole. It is a low, soft, prolonged tone, and is most distinctly heard over the fifth intercostal space.

The second sound is heard at the moment when the two sets of semilunar valves are closed and made tense, that is,

* A flexible stethoscope to listen to one's own heart-sounds can easily be made by fitting the mouthpiece to one end of a piece of rubber tubing about 18 inches long, and to the other end the bowl of a wooden pipe. The bowl is applied over the different regions of the heart, and the mouthpiece firmly fitted in the ear.

when the blood ceases to escape from the ventricles. It is a sharp, short sound, and is best heard at the second costal cartilage on the right side.

The cause of the first sound is not so evident. Possibly several factors aid in its production. The principal events occurring at the same time as the first sound may be enumerated thus :—

1. The heart's impulse.
2. The rush of blood into the arteries.
3. The contraction of the heart-muscle.
4. The sudden tension of the ventricular chambers and the auriculo-ventricular valves.

It has already been seen that the heart's *impulse* is caused by a sudden change in shape and density of the muscle and not by a knock against the chest. The first sound is heard more clearly when the chest wall is removed, so that the apex beating against the thorax cannot help to cause the sound.

The character of the sound is quite unlike that which could be produced by the *passage of the blood* through the arterial orifices.

The sound is not unlike the *muscular tone* which accompanies the continuous (tetanic) contraction of the skeletal muscles. It corresponds in time with the contraction of the cardiac muscle. In disease where the heart muscle is weak, the sound becomes faint or inaudible, although the valves are made tense by an intraventricular force sufficient to overcome the pressure in the arteries. Otherwise the circulation would cease. An abnormal præsystolic sound, like in character to the systolic sound, is now supposed by some physicians to be produced by the auricular systole ; but this cannot depend on the vibrations of valves.

All this evidence tends to show that the sound is produced by the contraction of the muscle tissue of the heart, or, in short, that it depends upon some sudden physical change occurring during the cardiac muscle contraction.

Against the view that the muscular tone is the cause of the first sound is urged the supposition that only tetanus causes a muscle-sound, and a single contraction is not accompanied by any tone. Though in many ways it differs from the single contraction of other muscles, yet the heart-beat is no doubt a single contraction. But the tone which may be heard during the normal contraction of skeletal muscle has not been proved to depend on regularly recurrent contractions such as occur in the tetanus produced by an interrupted

current; and a kind of thud very like the first sound of the heart may be elicited by the single stimulation of a skeletal muscle.

On the other hand the *auriculo-ventricular valves are made tense* at the beginning of the sound, and injury or disease of these valves is said to be associated with a weak or altered first sound: this is often observed in disease of the mitral valve. The blood is said by some to be necessary for the production of the sound, because the gentle closure and immediate subsequent tension of these valves have a share in causing it.

As before remarked, the valvular tension would not account for the præsystolic sound occasionally heard, and there is no doubt that the first sound can be heard in an empty heart removed from the animal in which the valves cannot become tense, or even in the ventricles after they are separated from the valves.

The sound has been analysed with suitable resonators, and two distinct tones made out: one high and short, corresponding to the tension of the valves; the other long and low, corresponding in duration with the muscle contraction.

The reasons given for thinking that the heart muscle cannot produce a tone suggest that the sudden state of tension of the ventricular wall when tightened over the blood may give rise to vibrations, and be an important item in causing the first sound. This would explain the faintness of the sound, both when the valves were injured and the muscle weak, and when the blood was prevented from entering. It would also explain the præsystolic sound, which requires a certain auricular tension for its production.

From the foregoing statements it would appear probable that both the tension of the valves and the muscle are concerned in the production of the first sound.

The production of the *second sound* is more easily explained. Occurring just after the ventricle is emptied, it is synchronous with the closure and sudden tension of the semilunar valves at the aorta and pulmonary orifices. The blood in the aorta forcibly closes the valves as soon as the ventricular pressure begins to wane. This sudden motion causes a vibration of the valves, which is rapidly checked by the continuons pressure of the column of blood.

Innervation of the Heart.

A most interesting phenomenon in the heart's action, and one difficult to explain, is the wonderful regularity of its rhythmical contractions under normal circumstances, and the extreme delicacy of the nervous mechanism by which it is regulated.

The vast majority of the active contractile tissues of the higher animals is under the immediate direction of the central nervous system. Thus the skeletal muscles are connected with the cerebro-spinal axis by means of nerves, along which impulses pass stimulating the contractile tissue to action.

Some muscular organs, as has been seen in the pharynx, œsophagus, &c., though not under the control of the will, are governed altogether by the cerebro-spinal axis ; while others, of which the most striking example is the heart, have, in immediate relation to the tissue, nerve elements capable of exciting them to contraction.

It will materially help us in comprehending the nervous mechanisms of the heart if we bear in mind the fact that the muscle tissue of the heart of some animals has—quite independently of any nervous influences—an inherent tendency to rhythmical contraction. This is shown by the following facts. The heart-muscle cannot, under any circumstances, remain contracted like a skeletal muscle in tetanus, or like an unstriated muscle in tonus, except when its tissue is spoiled by deficient nutrition, &c. The heart of many of the invertebrate animals contracts rhythmically without any nerve elements being found in it by the most careful microscopic examination. A strip cut from the ventricle of the tortoise can, by rapid gentle excitations, be made to beat with an automatic rhythm without the help of any known nerve mechanism. The lower part of the frog's ventricle—which is commonly admitted not to contain any nerves—beats quite rhythmically if stimulated with a gentle stream of serum and weak salt solution. There is no reason to assume that we cannot concede to muscle tissue, as we do to nerve cells, the property of acting with an automatic rhythm.

Although the heart-muscle may itself have this tendency to rhythmical contraction, there is no doubt that in all vertebrate animals the rhythm is controlled and regulated by nerves. These may be divided into an *intrinsic* and *extrinsic* set.

Intrinsic Nerve Mechanisms.

In cold-blooded animals, such as a frog or tortoise, the heart will beat for days after its removal from the animal, if it be protected from injury and prevented from drying. In warm-blooded animals the tissues lose their vitality very soon after they are deprived of their blood supply ; however, spontaneous rhythmical movements can be seen in the mammalian heart if removed at once after death. The hearts of oxen, rapidly slaughtered, give a few beats after their

removal from the thorax. If a blood current be caused to flow through the vessels of the heart tissue this spontaneous contraction will go on for some time, or will even recommence after having ceased.

The hearts of two criminals who were hanged were found to continue to beat for four and seven minutes respectively after the spinal cord and the medulla had been separated.

These facts prove conclusively that the stimulus which causes the heart to beat rhythmically arises in the muscle tissue of the organ or in close relation to it. Upon physiological grounds alone we might conclude that in the heart tissue of the vertebrata there exist nerve elements capable of sustaining the rhythmical action, even if we had not anatomical proof of the existence of the ganglionic cells with which we are familiar.

Such collections of nerve elements are called *automatic* centres, and are made up, like all other origins of nerve force, of ganglionic cells.

Since the heart of mammalian animals soon ceases to beat, it forms an unsatisfactory subject for experimental inquiry. The heart's innervation is, therefore, best studied in a cold-blooded animal, where also the mechanisms are probably more simple.

The frog, being readily obtainable, is commonly chosen.

After the cycle of the heart's beat has been carefully watched *in situ*, and when removed from the animal, if the apex of the ventricle be separated from the auricles and sinus venosus and not stimulated in any way, it remains motionless, while the auricles continue to beat. But it responds by an ordinary single contraction to short direct stimulus, and if the stimulus be kept up it beats rhythmically. If the auricles be removed from the ventricle so as to leave the line of union attached to it, both continue to beat. But each part beats with a different rhythm, and under like conditions the auricles continue to beat longer than the ventricles. If the heart be made into three zig-zag strips by a couple of partial transverse incisions, the rhythm of the sinus is carried by the muscle tissue to the very apex (Engelmann).

The auricles beat even when subdivided; and the dilated termination of the great vein, called the sinus venosus, opening into the right auricle, when quite separated from the rest of the heart, continues to beat longer and more regularly than any other part. When the entire heart is intact this sinus seems to be the starting point of the heart-beat.

This experimental evidence of the presence of nerve centres in

certain parts of the heart-muscle of the frog is supported by the results of anatomical investigations, for the microscope shows that there are many ganglionic cells distributed throughout the heart-

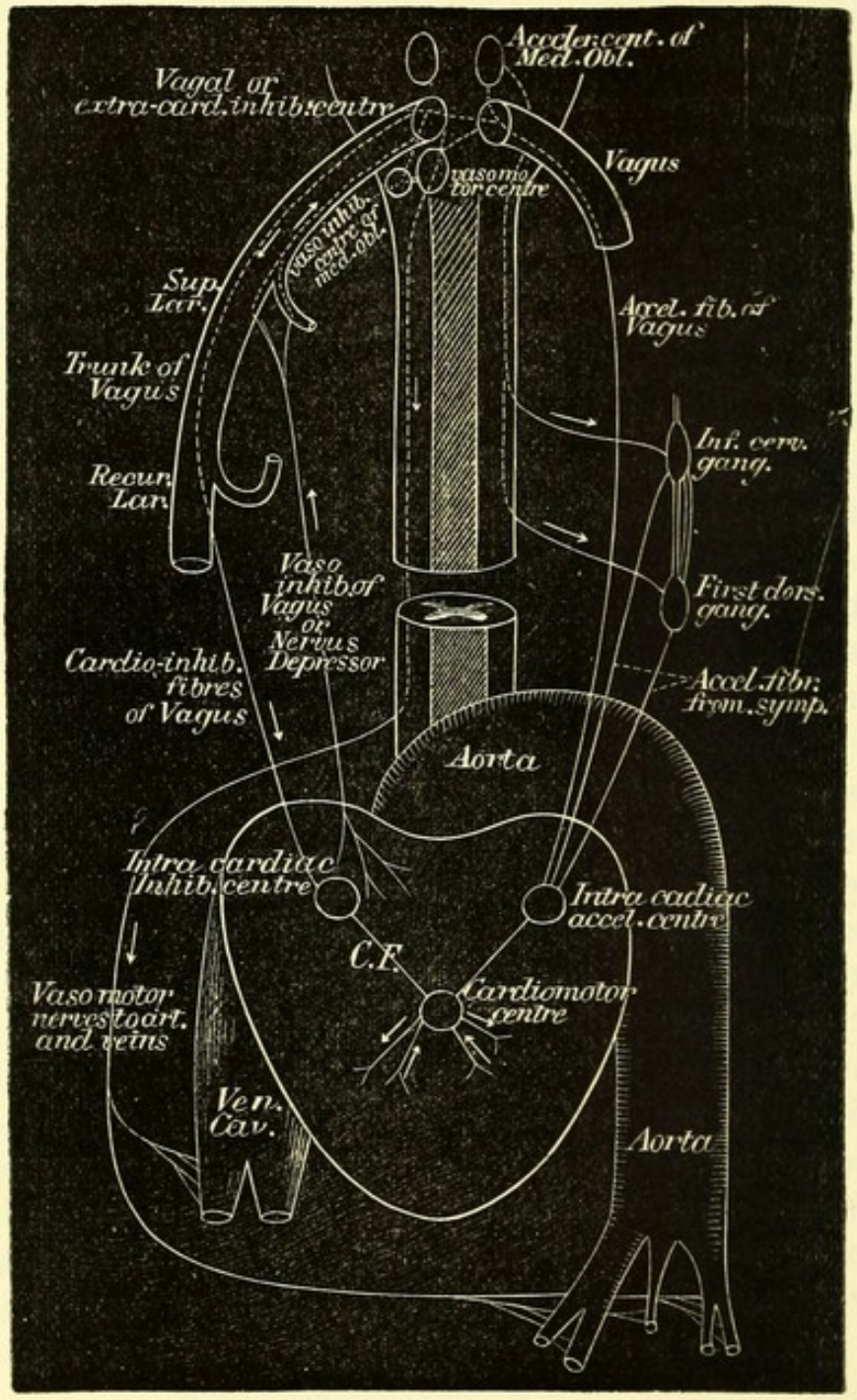


Fig. 122.—Diagrammatic Plan of the Cardiac Nerve mechanism. The direction of the impulses is indicated by the arrows. The right and left sides of the figure are used to show one half of the fibres.

tissue, and that they are located just where we should expect from the above facts. That is to say, there are none in the substance of the ventricles, while there are several groups of cells scattered around its base in the auriculo-ventricular groove (Bidder). There

are others in the walls of the auricles, particularly in the septum, and the greatest number are found in the walls of the sinus venosus (Remak).

The ganglia in the sinus venosus are most easily stimulated, and are probably the only ones which habitually act as automatic centres. They certainly take the initiative in the ordinary heart-beat, and regulate the rhythm of the contraction of the auricles and ventricles.

This seems more than probable from the following facts :—1. The ordinary contraction wave starts from the sinus venosus. 2. This part beats longer and more steadily than the others when separated from the animal. 3. When cut off from the sinus the beat of the heart becomes weak, uncertain, and changes its rhythm. 4. When the sinus venosus is physiologically separated by a ligature from the auricles and ventricle, both the latter cease to beat, while the motions of the sinus continue. If a slight stimulus, such as the touch of a needle, be then applied to the auriculo-ventricular margin, it gives rise to a series of rhythmical contractions. Or if the ventricle be separated from the auricles by incision through the auriculo-ventricular groove, the former commences to beat rhythmically, while the auricles commonly remain motionless.

These latter observations (experiments of Stannius) have been explained in various ways, supposing the ligature either (1) to excite some inhibitory nerve mechanism, or (2) cut off the exciting influence of the sinus. The most probable explanation seems to be the following. When cut off by ligature from the sinus venosus, the heart fails to contract spontaneously because the initiatory stimulus which habitually arrived from the sinus by means of the conducting power of the muscle-tissue, can no longer pass the block in that tissue. When the ventricle is cut away from the auricles, the incision is sufficient stimulus to the cells in the groove to make them excite its rhythmical contractions.

Although we cannot adequately explain the relationships borne by the different sets of ganglia in the frog's heart to one another, there seems no doubt that the following conclusions may be accepted as proven, and are, in all probability, applicable to the hearts of mammals. That nerve centres exist in the muscle tissue of the heart, some of which are capable of originating stimuli for the rhythmically contracting muscle. That there exist other ganglionic groups which help to regulate and distribute the stimuli in sequence throughout the several cavities.

Extrinsic Cardiac Nerves.

The intrinsic nerve mechanism of the heart just described is under the immediate control of the great nervous centres through the medium of fibres passing from the medulla oblongata by the vagus and sympathetic nerves.

Some of these fibres *check* the action of the intrinsic ganglia, and cause the heart to beat more slowly; hence they are called *inhibitory*. Others *quicken* the beat, and are called *accelerator*y.

Inhibitory Nerves of the Heart.

It was observed by Weber (1) that electric stimulation of the vagus nerve caused a slowing of the heart's rhythm, and if increased gave rise to a standstill of the heart in diastole; (2) that the heart-

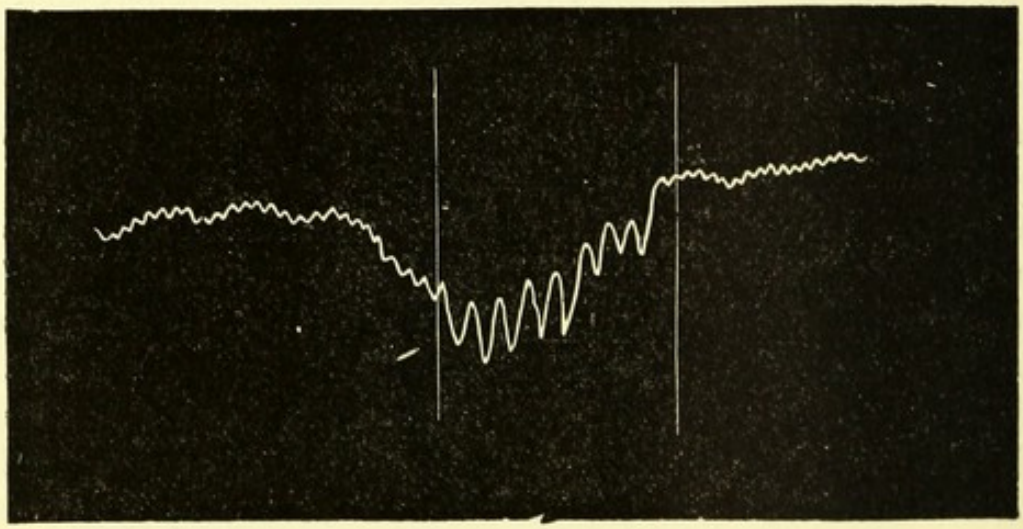


Fig. 123.—Tracing, showing the effect of weak Stimulation of Vagus Nerve. Stimulus applied between vertical lines. (Recording surface moved from left to right.)

beat gradually recommenced soon after the stimulus had been removed.

On the other hand (3) the section of both vagi produced an increase in the rapidity of the heart-beat, varying according to the kind of animal experimented upon. Section of only one vagus, however, has not this effect.

From these experiments it would appear—1. That some fibres of the vagus bear impulses of a checking or inhibitory nature to the intrinsic nerves of the heart. 2. That these influences are constantly in operation, or in other words, the vagi exert a tonic inhibitory influence on the rapidity of the heart-beat. 3. The tonic action of

one vagus bears inhibitory influence sufficient to regulate the heart's action. This tonicity of the vagus inhibition is more marked in dogs and man than in rabbits, and is reduced to a minimum in frogs, where section of the vagi produces very little effect on the rate of the beat.

Vagus inhibition is increased by the following circumstances—(*a*) certain psychical phenomena such as terror, which may produce a temporary standstill; (*b*) deficiency of arterial blood in the medulla oblongata; (*c*) increase of the blood pressure within the cranium; and (*d*) reflexly by the stimulation of many afferent nerves, particularly those bearing impulses from the abdominal viscera to the medulla, and the afferent fibres of the opposite vagus.

The following drugs affect the cardiac nerve mechanisms:—*Muscarin* produces diastolic standstill of the heart by exciting the local inhibitory ganglia or vagus terminals. *Atropin* causes quickening of the heart's action by paralysing the endings of the vagus, and also those intrinsic mechanisms which are supposed to have an inhibitory effect. *Nicotin* produces at first a slowing of the heart by stimulating the inhibitory tone of the vagus. This is soon followed by exhaustion of the terminals and a consequent quickening of the heart-beat. Large doses of *curare* paralyse the inhibitory fibres. *Digitalis* excites the vagus centre in the medulla, and thereby reduces the rapidity of the heart's beat.

The Accelerator Nerves.

It has been found that stimulation of the cervical portion of the spinal cord causes quickening of the heart-beat. This occurs even after the possibility of increase of blood pressure has been removed by section of the splanchnic nerves, and the tonic inhibition of the vagi has been cut off by their section. In the cervical portion of the spinal cord nerve channels must exist which are capable of stimulating the muscle fibres of the heart, so as to cause it to beat more quickly. These accelerator fibres pass from the cord through the communicating branches to the last cervical or first dorsal sympathetic ganglion, and thence to the heart. Stimulation of the ganglia, or of the branches passing thence to the heart, quickens its beat. The effect of stimulus applied to these nerves does not begin to show itself until a comparatively long time after it has been applied, and the acceleratory effort continues for a considerable time after the stimulus is removed. Stimulation of the accelerator fibres has less

effect than the inhibition of the vagus, which follows stimulation whether the accelerators are stimulated or not, while the action of the accelerators is suspended so long as the vagus is being stimulated.

An analogy exists between the nervous mechanism of the heart and that of the blood-vessels (to be described in a future chapter) which may help in their better comprehension. Both the heart and vascular muscles can work automatically ; though no ganglionic cells can be found in the latter. Both are regulated by central influences. The heart receives constant inhibitory dilator impulses by the vagus, and occasional motor (accelerator) impulses by the sympathetic. The vessels receive constant motor (constrictor) impulses by the sympathetic and occasional inhibitory (dilator) impulses from other nerves.

The motor influences are supposed to act by increasing the chemical activity of the tissue (anabolic action), while the inhibitory impulses lessen the tissue change (katabolic action).

Afferent Cardiac Nerves.

Besides the nerve channels bearing impulses to the heart, others pass from the heart to the medulla, probably having their origin in the inner lining of the heart, which is the part most sensitive to stimulus.

These fibres appear to be of two kinds, one of which (in vagi) affects the cardio-inhibitory centre and diminishes the pulse rate ; the other (depressor) affects the vaso-inhibitory centre and lowers the blood pressure. Increase of the intra-ventricular pressure stimulates both these sets of fibres, and thus we see that over-filling of the heart from increase of blood pressure, &c., causes retardation of its beat, and an equilibrium is established between the general blood pressure and the force of the heart-beat.

CHAPTER XVII.

THE BLOOD VESSELS.

THE channels which carry the blood through the body form a closed system of elastic tubes, which may be divided into three varieties :—

1. Arteries.
2. Capillaries.
3. Veins.

The arteries and veins serve merely to conduct the blood to and from the capillaries, where the essential function of the blood, *viz.*, its chemical interchange with the tissues, is carried on.

ARTERIES.

The *arteries* are those vessels which carry the blood from the heart to the capillaries. The great trunk of the *aorta*, which springs from the left ventricle, gives off a series of branches, which in turn subdivide more and more freely in proportion to their distance from the heart. Arterial twigs of considerable size here and there form connections with those of a neighbouring trunk (*anastomoses*) ; but these unions are simple junctions of single branches, never so complex as to be worthy of the name of a network or plexus, such as those seen in the capillaries or in the veins.

The *walls* of the arteries are made up of three coats :—

1. An *external* tough layer of white fibrous tissue, which gives strength to the vessels, restricts their elasticity like the webbing in the wall of rubber water-hose, and also acts as a bond of union between them and the neighbouring tissues. This coat (*tunica adventitia*) carries the minute vessels, necessary for the nutrition of the vessel wall, and nerves.

2. The *middle* coat (*tunica media*) forms the more characteristic part of the arterial structure, being a mixture of elastic tissue and unstriated muscle. It is much thicker in the arteries than in the

veins, where its special functions are not required. It differs some what in character in arteries of different calibre, being much thicker

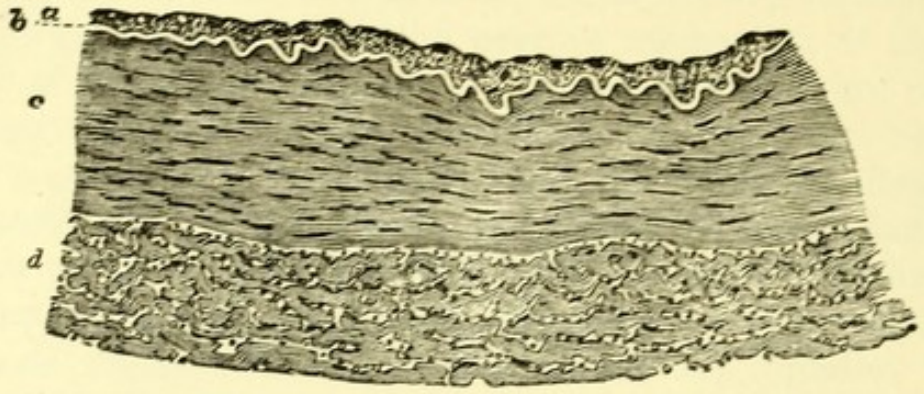


Fig. 124.—Transverse Section of part of the Wall of the Posterior Tibial Artery (man). (Schäfer.)

(*a*) Endothelium lining the vessel, appearing thicker than natural from the contraction of the outer coats.
(*b*) The elastic layer of the intima.
(*c*) Middle coat composed of muscle fibres and elastic tissue.
(*d*) Outer coat consisting chiefly of white fibrous tissue.

in the large vessels. This change occurs gradually on passing along the diminishing branches. In the large arteries and the arterioles the middle coat differs essentially both in structure and in function, and in each class of vessel it forms the most important part for the due performance of their respective functions. In the large vessels it is made up of fibres and sheets of elastic tissue woven into a dense felt-work, interspersed with a few muscle cells. In the smallest arteries or arterioles, on the other hand, the great mass of the middle coat is made up of muscle cells, the elastic tissue being but sparsely represented. Between the large arteries and the capillaries every grade of transition may be found; the elastic tissue gradually becoming less abundant and the muscle elements relatively more numerous in proportion as the capillaries are approached.

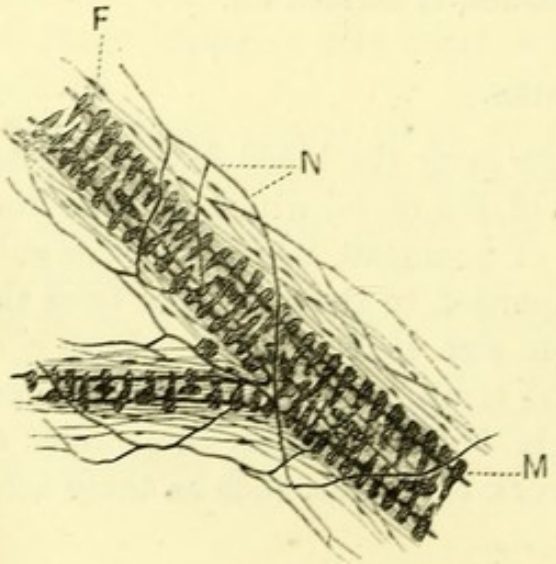


Fig. 125.—Portion of Small Artery from Submucous Tissue of Mouse's Stomach, stained with gold-chloride, showing the nuclei of the muscle cells (M) passing transversely around the vessel to form the middle coat, outside which is the fibrous tissue of the outer coat (F). Around the vessel several fine nerve fibrils form a network (N).

3. The *internal* lining (*tunica intima*) of the arteries is composed of a delicate, elastic, homogeneous membrane, lined with a single layer of endothelial cells. The intima may be said to be continuous throughout all the vessels and the heart cavities.

It is thus seen that the large arteries have extremely elastic and firm walls, capable of sustaining considerable pressure. The smaller the calibre of the arteries becomes the more the general property of elasticity and resiliency is reinforced by that of *vital contractility* due to the greater relative number of muscle cells contained in the middle coat.

Capillaries.

The frequently branching arterioles finally terminate in the *capillaries*, in which distinct branches can no longer be recognised,

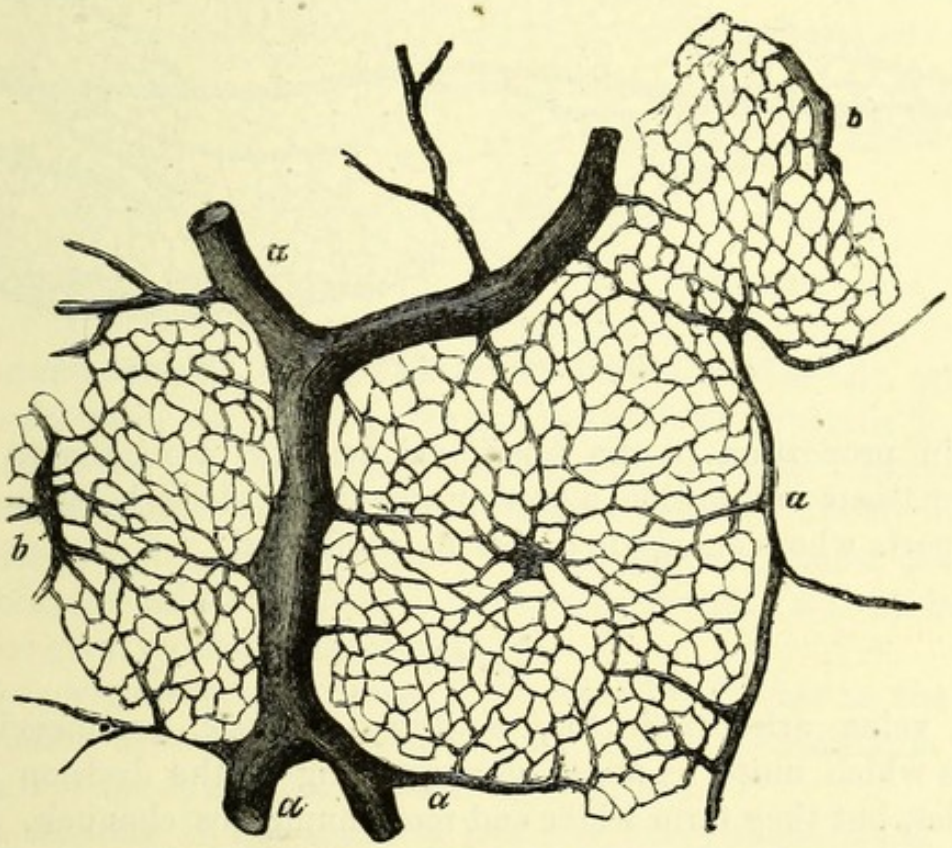


Fig. 126.—Capillary network of a Lobule of the Liver.

but the thin canals are interwoven into a network of blood channels, the meshes of which are made up of vessels all of which have about the same calibre. They communicate indefinitely with the capillary meshworks of the neighbouring arterioles, so that any given capillary area appears to be one continuous network of tubules, connected here and there with the similar networks from distinct arterioles, and thus any given capillary area may be fed with blood from several

different sources. The walls of the capillaries are composed of a single layer of elongated endothelial cells (possibly lining an invisible membrane) cemented edge to edge to form a tube. They are soft and elastic, and permeable not only to the fluid portion of the blood, but also, under certain circumstances, to the corpuscles.

It is, in fact, in these networks that the essential function of the circulation is carried on, viz., the establishment of a free interchange between the tissues and the blood.

The characters of the capillary network vary in the different tissues and organs; the closeness and wideness of the meshes may be said

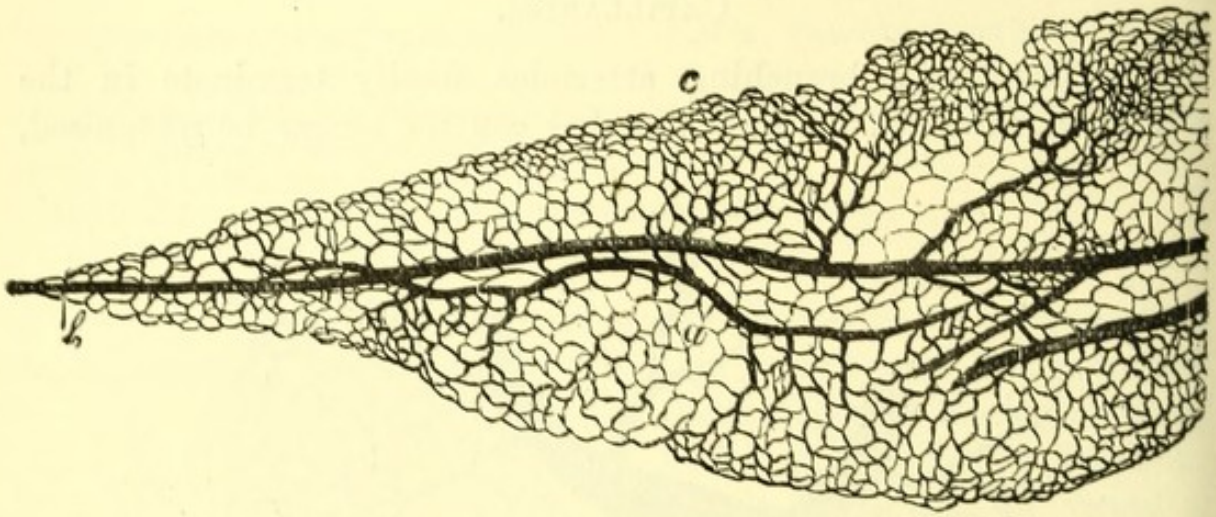


Fig. 127.—Capillary network of Fat Tissue. (Klein.)

to be in proportion to the functional activity or inactivity of the organ or tissue in question, a greater amount of blood being required in the parts where energetic duties are performed.

Veins.

The veins arise from the capillary network, commencing as radicles which unite in a way corresponding to the division of the arterioles, but they form wider and more numerous channels. They rapidly congregate together to make comparatively large vessels, which frequently intercommunicate and form coarse and irregular plexuses. The general arrangement of the structures in the walls of the veins is like that of the arteries; they also have three coats, the *external*, *middle*, and *internal*; the tissues of each differing but little from those of the arteries. The *external* coat is like that of the arteries, but is not quite so strong. The *middle coat*, however, in the large veins, is easily distinguished from that of the large arteries by being much thinner, owing to the paucity of yellow elastic tissue.

It is also characterised by its relative richness in muscle fibre. The structure of the middle coat of the small veins can be distinguished from that of the arterioles by the comparative sparseness of the muscle cells running around the tubes. The inner coat of the veins is practically the same as that of the arteries.

The veins are capable of considerable distension, but, though possessed of a certain degree of elasticity, they are much inferior to the arteries in resiliency.

In a large proportion of veins, *valve-like folds* of their lining coat exist, which prevent the backward flow of blood to the capillaries and insure its passage towards the heart. These valves resemble in their general plan the pocket valves that protect the great arterial orifices of the heart. They vary much in arrangement, there being commonly two or sometimes only one flap or pocket entering into the formation of the valve. They are closely set in the long veins of the extremities, in which the blood current has to move against the force of gravity.

Aggregate Sectional Area of the Vessels.

The general aggregate diameter of the different parts of the vascular system varies greatly. The combined calibre of the branches of an artery exceeds that of the parent trunk, so that the aggregate sectional area of the *arterial tree* increases as one proceeds from the aorta towards the capillaries. After the muscular arterioles are passed the general diameter of the vascular system suddenly increases immensely, and in the *capillaries* it reaches its maximum, the aggregate sectional area of which is said to be several (5 to 8) hundred times as great as that of the aorta.

The aggregate sectional area of the *veins* diminishes as the tributaries unite to form main trunks, and reaches its minimum at the entrance of the vena cava into the right auricle.

The capacity of the veins is, however, everywhere much greater than that of the corresponding arteries, the least difference being near the heart, where the calibre of the venæ cavæ is more than twice that of the aorta.

After this brief anatomical sketch the most important properties of each part of the vascular system may be summarised thus :—

1. The structure of the walls of the large arteries shows them to be capable of sustaining considerable pressure, and of exerting powerful and continuous *elastic recoil* on the blood.

2. In the small arteries, as well as this elasticity, frequent variation in their calibre occurs, dependent on the *contraction* of their muscular coat which regulates the blood-flow.
3. In the capillaries we find extreme thinness, elasticity, and *permeability* of their wall, which presents an *immense surface*, so as to allow free interchange between the blood and the surrounding textures.

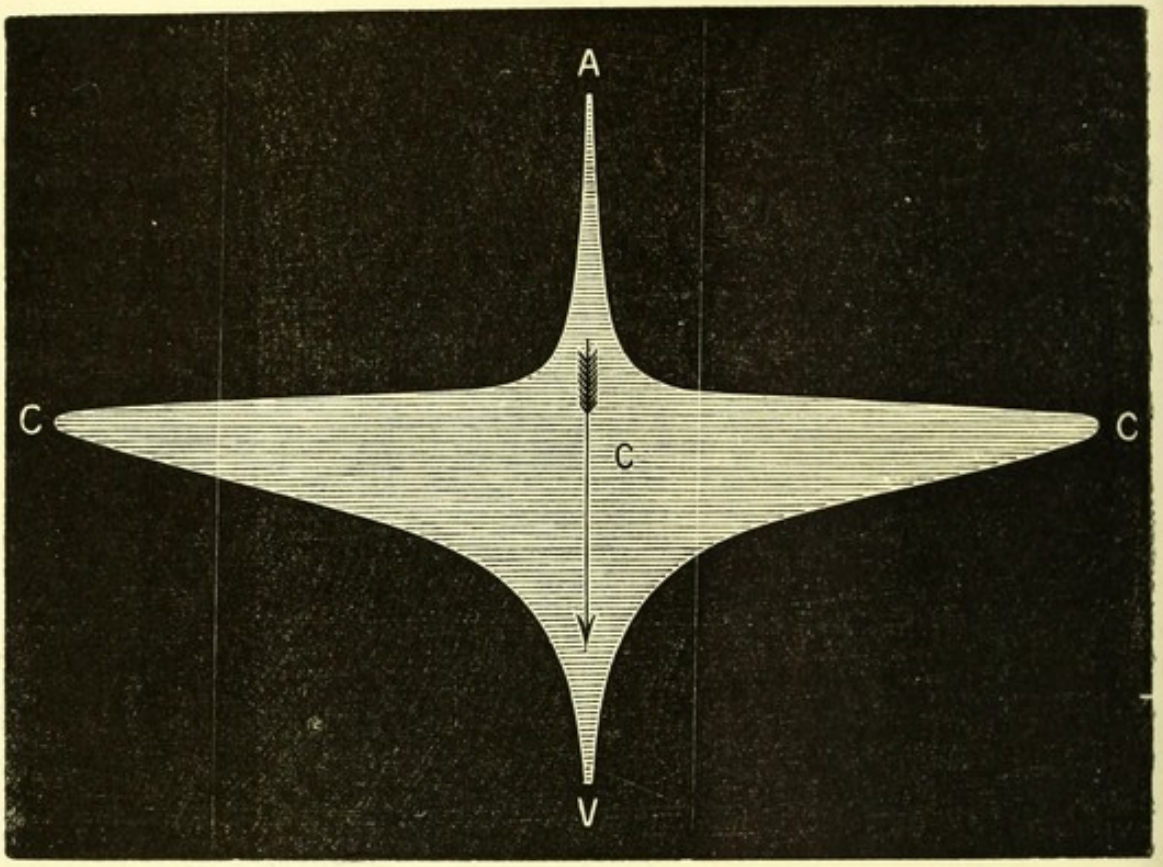


Fig. 128.—Diagram intended to give an idea of the aggregate sectional area of the different parts of the vascular system.

A. Aorta. C. Capillaries. V. Veins.

The transverse measurement of the shaded part may be taken as the width of the various kinds of vessels, supposing them fused together.

4. The veins have yielding and distensible walls, capacity to accommodate a large quantity of blood, and *valves* to prevent its backward flow upon the capillaries.
5. The aggregate sectional area of the systemic capillaries is about three hundred times that of the great veins, and seven hundred times that of the aorta, so that the current of the blood must be proportionately slower in the capillary network.

Physical Forces of the Circulation.

A liquid flows through a tube as the result of a difference of pressure in the different parts of the tube. The liquid moves from the part where the pressure is higher towards that where it is lower, except where sudden and great variations of calibre occur.*

The energy of the flow corresponds with the amount of difference in the pressure, and varies in proportion to it, being continuous so long as the pressure is unequal in different parts, and ceasing when it is equalised throughout the tube.

If liquid be forcibly pumped into one extremity of a long tube, such as a garden-hose, a pressure-difference is established, the pressure becoming greater at the end into which the liquid is pumped, a current consequently takes place towards the open end. So long as the free or distal end of the tube is quite open and on the same level as the rest, no very great pressure can be brought to bear on the walls of the tube, no matter how forcibly the pumping may go on, as the liquid easily escapes, and therefore flows the more quickly as the pumping becomes more energetic. If, however, the outflow be impeded by raising the distal end of the tube to any considerable height, or by partially closing the orifice with a nozzle or rose, then the pressure within the tube can be greatly increased by energetic pumping, and the tube being elastic will be distended.

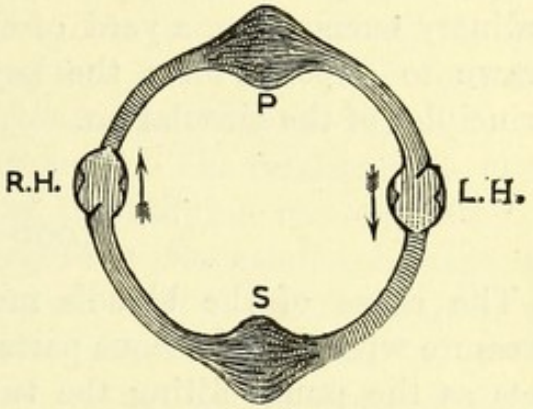


Fig. 129.—Diagram of Circulation, showing right (R.H.) and left (L.H.) hearts, and the pulmonary (P.) and systemic (S) sets of capillaries.

It can be further observed in this common operation that the smaller the orifice of the nozzle the greater the pressure in the tube with a given rate of working the pump; and, the orifice remaining the same, the pressure will increase in proportion as the pump is more energetically worked. Or in other words, the pressure within

* Although in the whole course of any system of tubes the flow of liquid must take place from the part of higher to that of lower pressure, yet if a narrow tube open abruptly into one the diameter of which for a short length is much greater, the diminution of velocity in the wide tube may cause the local pressure in it to exceed that in the narrower tube immediately preceding; so that the liquid would be actually flowing, for a short distance, from a point of lower to a point of higher pressure.

the tube will depend on (*a*) the energy used at the pump, and (*b*) the degree of impediment offered to the outflow.

If the tube be resilient, and the nozzle have a small orifice so that a high pressure can be established within the tube, it will be found that the liquid will flow from the nozzle in a continuous stream, and will not follow the jerks communicated by the pump. That is to say, the interrupted energy of the pump is stored up by the elastic tube and converted into a continuous *pressure* exerted on the fluid. But if the tube be quite rigid, or the orifice too wide to allow the pressure within the tube to be raised sufficiently high, then the fluid will flow out of the end of the tube in jets which correspond with the strokes of the pump ; *i.e.*, the outflow will follow closely the pressure difference caused by the pump at the point of inflow.

These simple facts, which can be verified experimentally with an ordinary enema bag, a yard of elastic tubing, and a short glass tube drawn to a point, form the key to the most important dynamic principles of the circulation.

Blood-Pressure.

The cause of the blood's motion is simply a difference in the pressure within the various parts of the vascular system, for the heart acts as the pump filling the tube represented by the large elastic arteries, which can be more or less distended, according as (1) the outflow is impeded or facilitated by the contraction or relaxation of the muscular arterioles which form the outlet, or as (2) the inflow is increased or diminished by the greater or less activity of the heart's action.

From the foregoing facts, and what has been said of the direction of the blood current, namely, that it flows from the arteries through the capillaries into the veins, it would appear that the pressure in the arteries exceeds that in the capillaries, and that in the capillaries must in turn be greater than that in the veins, the blood flowing in the direction in which the pressure becomes less.

The different manner in which blood flows from a cut artery and a cut vein shows that a great difference exists in the pressure within the two sets of vessels.

When a small artery is cut and the orifice directed upwards the blood spurts out two or three feet in jerks. When a vein is cut, the blood only trickles gently from the orifice, the force of the flow depending much upon the position of the part. It is well to remember that bleeding from a vein in the leg or arm can be stopped

by placing the limb in a position more elevated than the rest of the body, so as to prevent the force of gravity from acting on the blood.

By means of a special form of gauge (the mercurial manometer), —which will presently be described—the exact difference in the pressure exerted by the blood against the vessel-walls in the different parts of the circulation can be accurately estimated, and it has been found by direct experiment that the *pressure* varies, just as one would be led to expect from a consideration of its physical relationships, namely, with the *direction* and *rate* of the current and the varying *width of the bed* in which it flows.

The fall in pressure observed in the vessels when passing from the left ventricle to the right auricle is not even. In the arterioles it falls suddenly, and a great difference always exists between the arterial and venous pressure (v. p. 247). It is on account of the permanent high pressure in the arteries and comparatively low pressure in the capillaries and veins, that there is a continuous and permanent flow through the capillaries from arteries to veins.

Sustentation of the arterial blood-pressure.—The fundamental problem that must be clearly understood in studying the dynamics of the circulation is, how the high pressure in the arteries is kept up, or, in other words, how the arteries can exert so much pressure on the blood when the capillary out-flow is so wide and free.

From the description already given of the action of the heart, it appears that each *beat of the ventricle* pumps some six ounces of blood into the aorta. Though coming to the left ventricle from the pulmonary circulation, the blood may, on account of the exact co-operation of the two sides of the heart, be regarded as being pumped out of the systemic veins. Thus, as far as the general consideration of the physical forces is concerned, the pulmonary circulation may be left out of the question. This pumping occurs some seventy times a minute, so that a great quantity of blood is removed from the veins and forced into the arteries. The ventricles in filling the arteries have to work against considerable pressure, and may be said to pump up the blood from the low-pressure veins into the high-pressure arteries, and the result of this work is the different pressure in the two sets of vessels. During the contraction of the heart the ventricular pressure exceeds that of the aorta, while during the diastole it falls to that of the auricle or even of the great veins. The heart then is the most essential agent in keeping the arteries stretched and over-filled, and in emptying the veins.

The second important factor in enabling the high arterial blood-pressure to be kept up, is the *resiliency of the middle coat of the*

arteries. It is only on account of the great elasticity of their arterial walls, that these vessels are capable of being so over-filled, and because of the perfect resiliency of the elastic coat, that they are able to exert such powerful pressure on the blood for such an unlimited time. If the arteries were rigid tubes, to distend them with a fluid, itself inelastic, would of course be out of the question; the outflow from the distal extremity would only take place when the additional charge of blood was injected by the heart.

With each contraction the ventricle overcomes arterial pressure, and further stretches the elastic artery. The act of injecting the blood into the aorta only occupies about one quarter of each heart beat. The semilunar valves bear the pressure of the blood in the aorta for the rest of the time. The whole force of the ventricle is therefore used up in causing arterial distension. During the greater part of the heart's cycle, the arteries are closed at their cardiac end by the aortic valves, and open at their distal end to the capillaries.

As the result of this, the blood flows constantly out of the distended arteries, through the capillaries, into the veins, and tends to equalise the pressure in the veins and arteries.

But why does not this constant outflow allow the pressure in the arteries to fall to the level of that in the veins? Or in other words, what is the impediment offered to the escape of the blood that thus keeps the arteries distended? If the arteries and veins were a set of continuous wide tubes of similar construction and capacity throughout, it would be impossible for the heart to empty the veins, overfill the arteries, and establish the great pressure difference that normally exists. Therefore some resistance equal to the pressure must be offered to the flow of the blood from the arteries into the veins.

This *resistance* is made up of several items, of which one alone, namely, the vital contraction of the *arterioles*, is sufficient to keep up the arterial pressure. No doubt the great *increase of surface* over which the blood has to move in the capillaries, and the pressure exercised upon them by the *surrounding elastic tissues*, have influence in impeding the emptying of the arteries. But the contractility of the arterioles is the most important item, as may be seen from the following consideration. The resistance offered by the capillaries is insignificant when compared with the arterial blood-pressure, for the increase of friction accompanying their greater extent of surface is counterbalanced by the decrease of friction dependent upon the great *total* capacity of the capillaries in comparison with that of the small arteries. The capillary resistance alone is therefore not sufficient to

restrain the blood from rushing into the veins. This is seen when the arterioles are paralysed by the destruction of the nervous mechanism controlling them; the blood then flows readily through the capillary network, the veins become engorged, the arterial blood-pressure falls, and the circulation comes to a standstill, in spite of the heart's more rapid beats. We know that beyond the arterioles the pressure falls suddenly, and in the capillary network it is always very low.

The four great factors in keeping up the arterial blood-pressure may be thus enumerated: 1, the heart-beat; 2, perfect aortic valves;

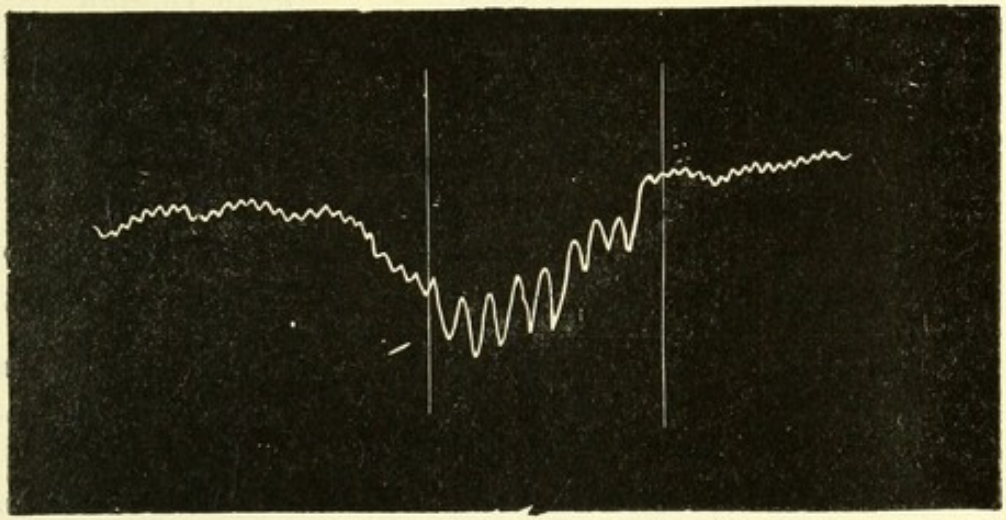


Fig. 130.—Tracing, showing the effect of weak Stimulation of Vagus Nerve. Stimulus applied between vertical lines. (Recording surface moved from left to right.)

3, the elastic resiliency of the large arteries; 4, the resistance offered by the contraction of the muscular arterioles.

Heart-beat.—If any factor fail, the mechanism of the circulation is at once impaired. For example, the heart's beat may be stopped by the stimulation of the inhibitory nerve fibres of the vagus, in which case the blood-pressure rapidly falls, as shown by the curve taken by the graphic method. Or weakness of the heart-beat may arise from disease (fatty degeneration) of the muscle, when signs of low arterial tension can be recognised in the human subject.

Valves.—Any insufficiency of the aortic valves that permits the blood to flow backward into the ventricle, allows the arterial pressure to fall between each ventricular systole, and gives rise to the characteristic "pulse of unfilled arteries" as it is called by the physician.

Elasticity of Arteries.—The resiliency of the arterial coats may also be destroyed to a certain extent by degeneration of the tissue, in which case the large arteries become greatly distended, and unable to exert their normal steady pressure on the blood.

Contractile Arterioles.—Injuries of the nervous centres are often associated with paralysis of the muscular arterioles, and fall of blood-pressure; but the effect upon the blood-pressure of dilatation of the small arteries can be best seen by experimenting on the nerves that control their contraction. If paralysis or inhibition of the vasomotor mechanisms be experimentally produced, the result on the arterial pressure is the same, a sudden fall, which may reach that of the atmosphere. The chief opposition to the outflow of blood from the arteries being removed, they cease to be tense, even though the ventricle continue to beat and pump the blood into them.

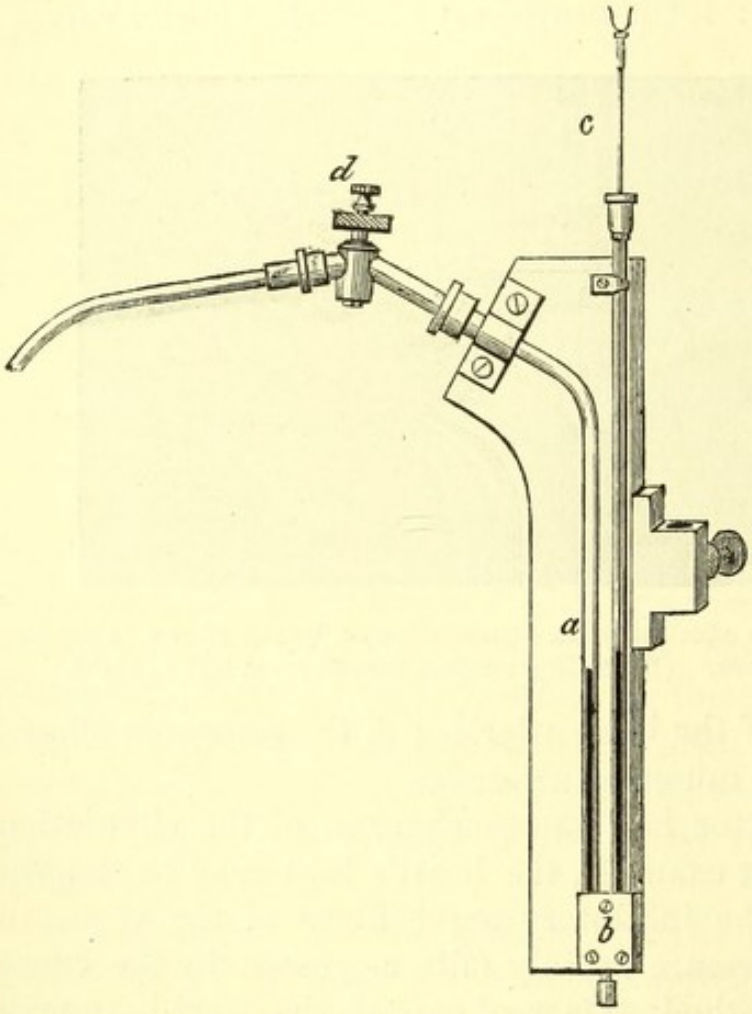


Fig. 131.—Mercurial Manometer for measuring and recording the blood pressure.

a. Proximate limb of manometer.
b. Union of two limbs of manometer.
c. The rod floating on mercury and carrying the writing point.
d. Stop-cock through which the sodium bicarbonate can be introduced between the blood and mercury of manometer.

Measurement of the Blood-Pressure.

The first attempt at direct measurement of blood-pressure was made by the Rev. Stephen Hales about the middle of last century, who, wishing to compare the motion of fluids in animals with that in plants, connected a tube with an artery of a living animal, and found that the blood was ejected with considerable force, and that when the artery of a horse was brought into union with a long upright tube, the blood reached a height of about three yards.

The column of blood is not now used as a measure, because so much blood leaving the vessels tends to empty them and to reduce the pressure in the arteries; besides the coagulation of the blood

soon stops the experiment. We now employ the mercurial manometer, which consists of a column of mercury in a U-shaped tube. To prevent coagulation, the tube between the mercury and blood is filled with a solution of sodium carbonate, the pressure being regulated to equalise as nearly as possible that of the blood. A rod is

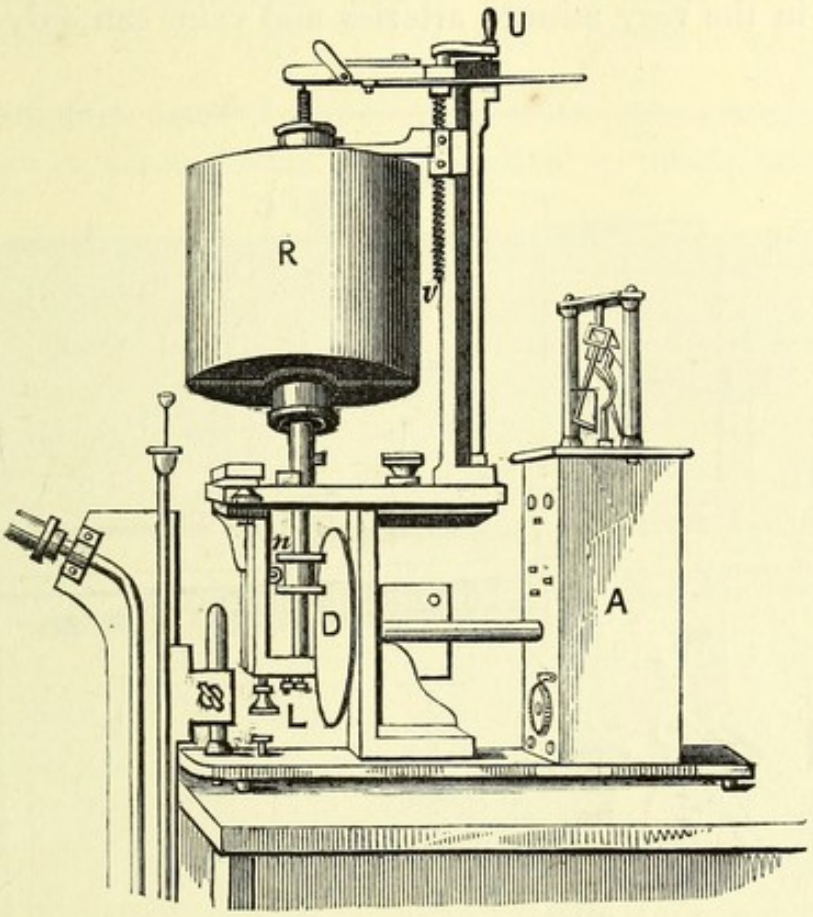


Fig. 132.—The ordinary modern form of rotating blackened cylinder (R), which is moved by clock work in the box (A) by means of the disc (D) pressing upon the wheel (*n*), which can be raised or lowered by the screw (L), so as to come in contact with any part of the disc more or less near the centre, and thus rotate at different rates. The cylinder can be raised by the screw (*v*), which is turned by the handle (U). (Hermann.)

made to float upon the mercury, in the open side of the tube, and to the upper extremity of this a writing apparatus can be attached, so that by the movements of the mercury, a graphic record of the blood-pressure and its variation can be traced on a regularly moving surface. This instrument, known as Ludwig's Kymograph, is that used in all ordinary measurements and experiments on blood pressure.

In order to overcome the inertia of the mercurial column, another manometer has been devised which will be mentioned in speaking of the character of the curve (p. 250). When an experiment of long

duration has to be made, a recorder with a rolled strip of paper can be employed (Fig. 133).

The modern accurate methods of research have taught us the differences in pressure that exist in the various parts of the vascular system. However, direct measurement can only be accomplished in vessels of such a size as to admit a cannula, hence the pressure in the capillaries in the very minute arteries and veins can only indirectly

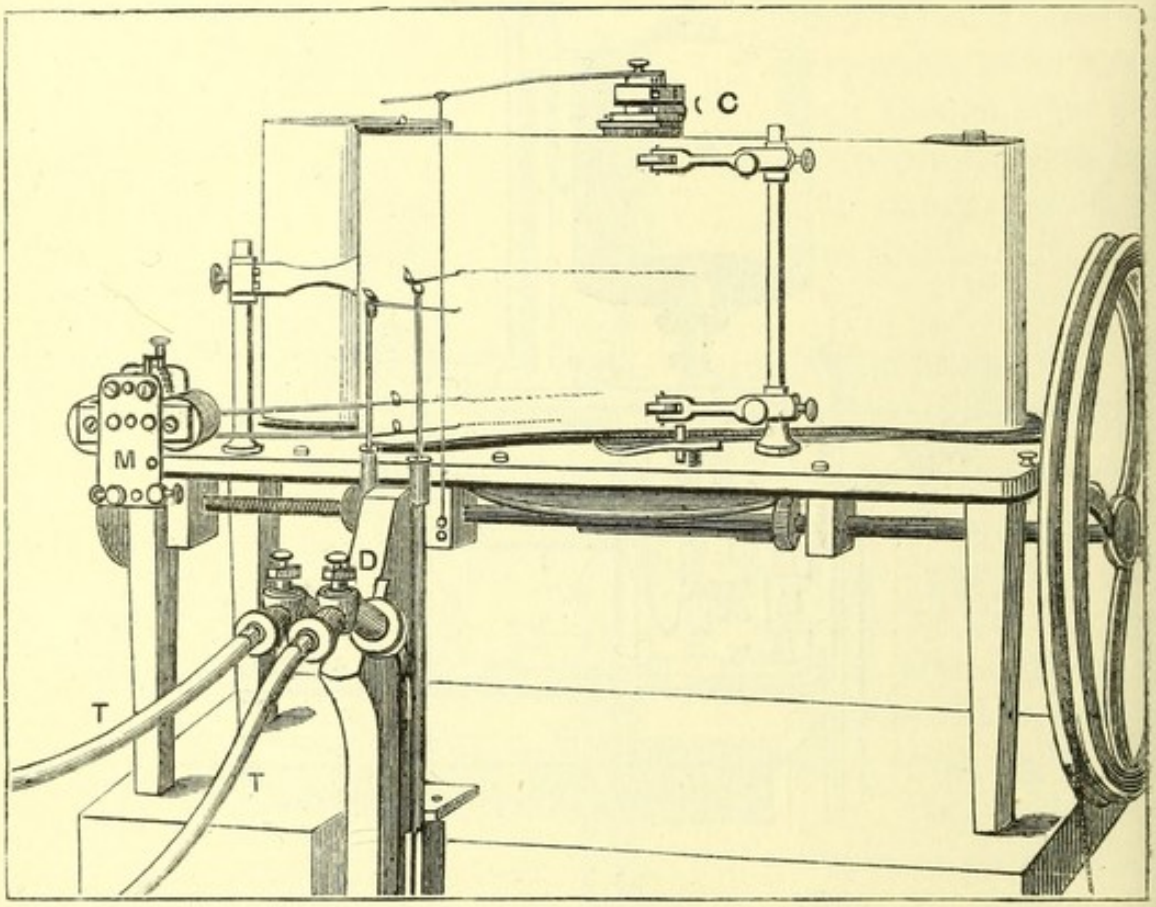


Fig. 133.—Ludwig's Kymograph with continuous paper.

The instrument consists of an iron table, above which the recording surface is slowly drawn past the writing points from an endless roll of paper on the left by the motion of the cylinder (c), and rolled up on a spindle next the driving-wheel on the right. The mercurial manometers are so fixed on (d) that the open ends come in front of the firm roller upon which the paper rests. The writing style can be seen rising from these tubes while the other limbs of the manometers lead through the stop-cocks to the tubes which are in communication with the blood-vessels. The time is recorded by means of a pen attached to the electro-magnet (m), which by a "breaking" clock, is demagnetised every second. The moment at which a stimulus is applied is marked on the zero line by a key to which another pen is attached near the time-marker.

be estimated. The pressure in all parts of the vascular system is subject to frequent variations to be presently mentioned, but this table may be useful in giving a general idea of the average permanent

differences that exist in the different vessels of large animals and man.

Large arteries (Carotid, Horse)	+ 160 mm.,	mercury.
Medium „ (Brachial, Man)	+ 120 mm.,	„
Capillaries of Finger,	+ 38 mm.,	„
Small Veins of Arm	+ 9 mm.,	„
Large Vein of Neck	− 1 to − 3 mm.,	„

If the different parts of the circulation be represented on the base line H. A. C. V., these letters corresponding to heart, arteries, capil-

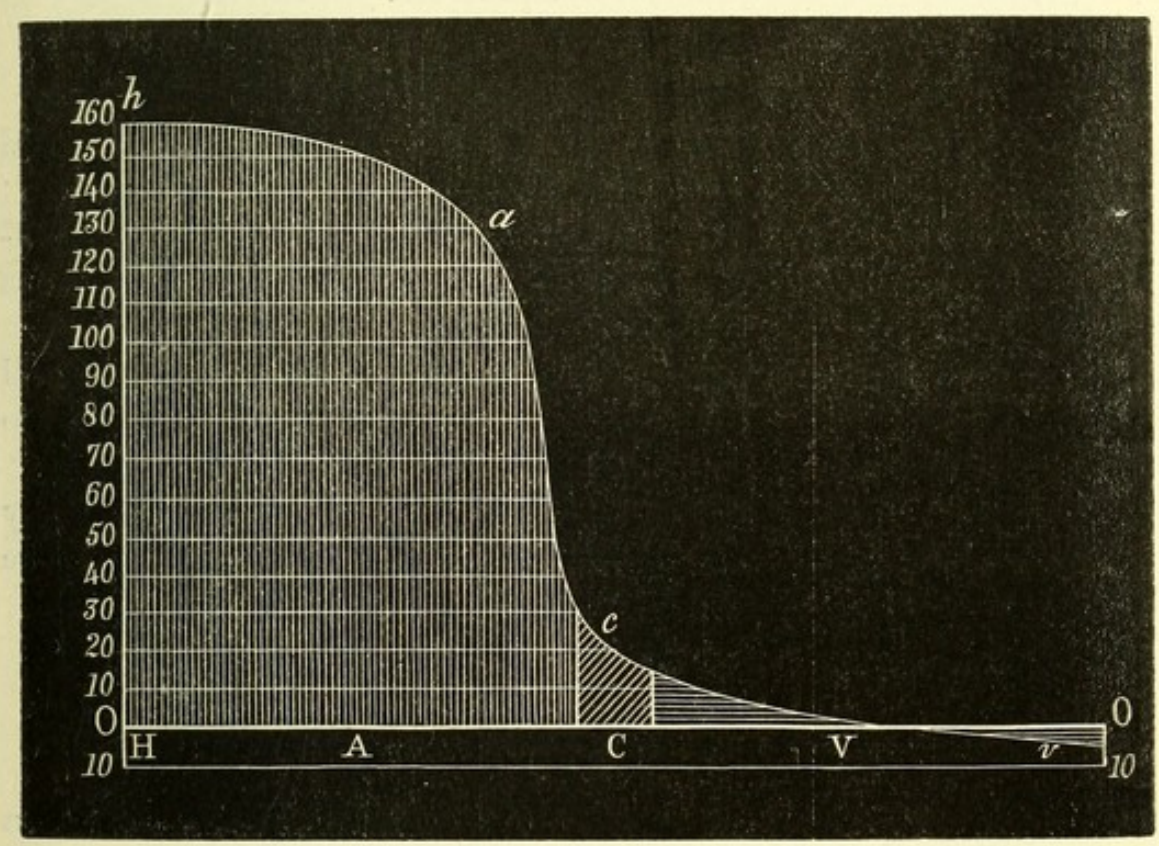


Fig. 134.—Diagram showing the relative height of the blood-pressure in the different regions of the vessels.

H. Heart. a. Arterioles. v. Small veins.
A. Arteries. c. Capillaries. V. Large veins.
H. V. being the zero line (= atmospheric pressure) the pressure is indicated by the height of the curve. The numbers on the left give the pressure (approximately) in mm. of mercury.

laries, and veins respectively, and if the height of the blood-pressure be represented on the vertical line in mm. Hg. the curve *h*, *a*, *c*, *v*, would give about the relative pressure in the various parts of the circulation. This shows that in the receiving chamber of the heart the pressure is negative, while the ventricular pump drives it to the height of the arterial pressure 160 mm. Hg. In the arteries the

pressure is everywhere high, while just before the blood reaches the capillaries, a sudden fall occurs. The variation after this is merely a gentle descent until the large venous trunks are reached, where the blood-pressure is below zero, *i.e.*, below the pressure of the atmosphere.

From a purely physical point of view the ventricle may be regarded as pumping the blood up to an elevated high-pressure reservoir of small capacity (the arteries), from which it rapidly falls by numerous outlets into an expansive low-lying irrigation basin (the wide capillaries), whilst it slowly trickles back to the well (the auricle), which lies below the surface pressure.

From this diagram the following points can be gathered :—

1. The great difference between the pressure on the arterial and venous sides of the circulation.
2. The comparatively slight difference in pressure in the different parts of the arterial or of the venous systems respectively.
3. The suddenness of the fall in the pressure between the small arteries and the capillaries, where the great resistance to the outflow is met with.
4. In the large veins the pressure of the blood is habitually below that of the atmosphere, only becoming positive during forced expirations.

Variations in the Blood-Pressure.

If the blood-pressure be recorded with Ludwig's Kymograph, a tracing will be obtained, which shows that the pressure undergoes periodic elevations and depressions of two different kinds. The smaller oscillations are found to correspond with the heart-beat, the larger waves have the same rhythm as the respiratory movements, and the average elevation of the mercurial column is spoken of as the *mean pressure*. In the large arteries of the warm-blooded animals, this mean pressure varies with the size of the animal from 90 mm., mercury, to more than 200 mm. In cold-blooded animals it is comparatively low, from 22 mm. in the frog, (Volkmann), to 84 mm. in a large fish.

The general mean pressure in the arteries is increased by : (1), increased action of the heart ; (2), increased contraction of the muscular coat of the arteries ; (3), sudden increase in the quantity of

blood. When the change is gradual, the vessels adapt themselves to the increase.

The opposite of these conditions may be said to have a contrary effect.

The character of the change in pressure which accompanies the heart's systole, is not shown exactly in the tracing obtained by the

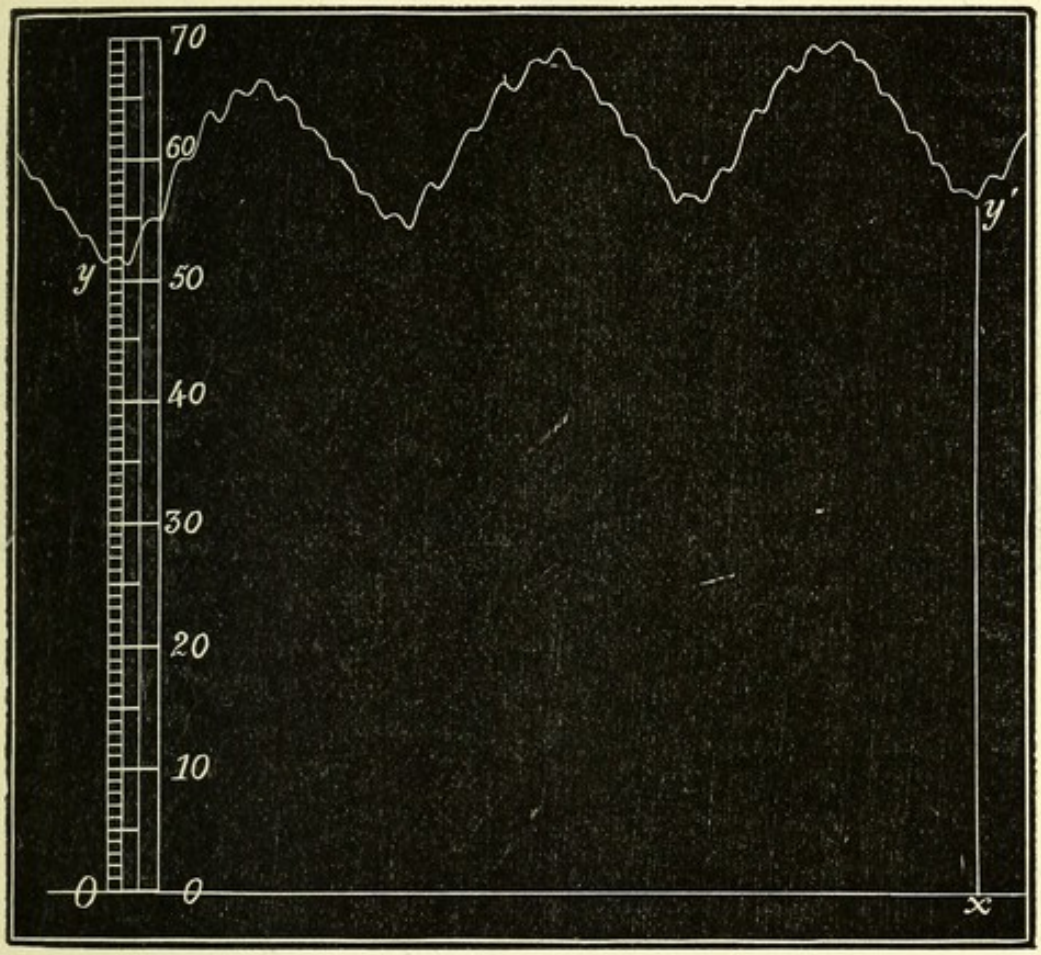


Fig. 135.—Blood-pressure Curve, drawn by mercurial manometer. $O-x$ = zero line $y-y'$ = curve with large respiratory waves and small waves of heart impulse. A scale is introduced to show height of pressure.

mercurial manometer, owing to the sluggishness of the movement of the mercurial column which, as it were, rubs off the apices of the curves. But with the *spring manometer* of Fick, the details of these oscillations are marked. They are of course synchronous with the arterial pulse, and follow the variations of tension, as will be described when treating of that subject. (See Figs. 136 and 137.)

Influence of Respiration on Blood-Pressure.

The explanation of the respiratory undulations in the tracing of the blood-pressure is difficult. Though many causes have been

assigned, no single one appears to explain adequately all the changes that may occur in this phenomenon. At first sight the respiratory

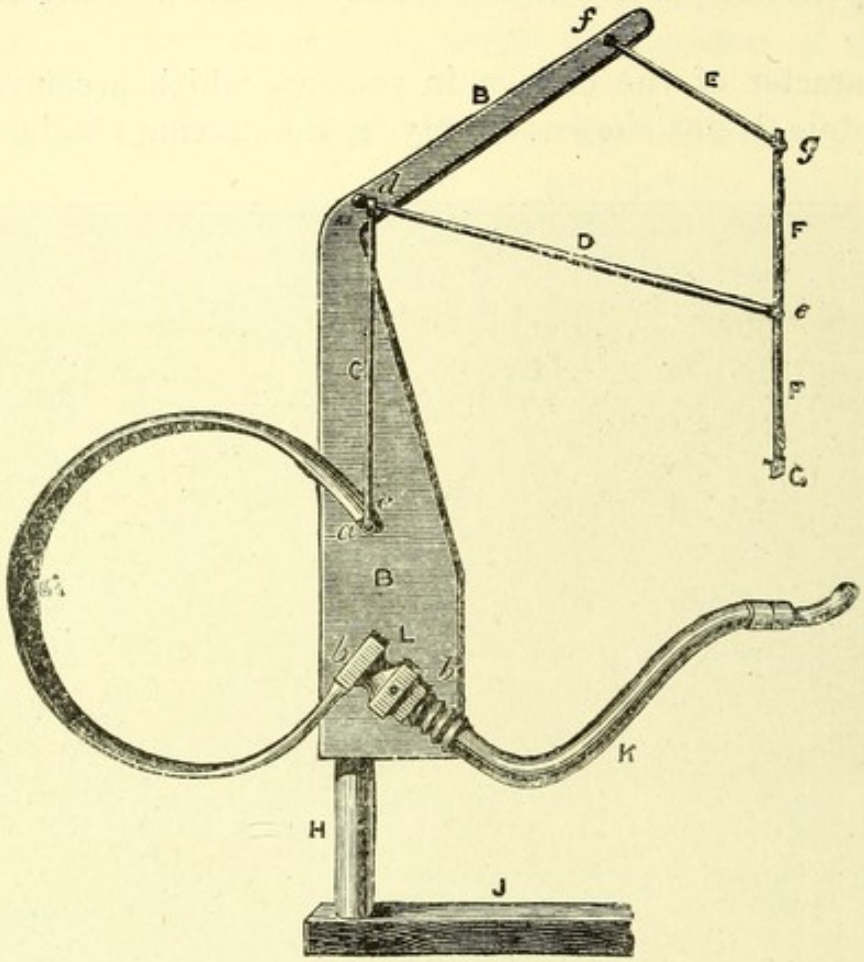


Fig. 136.—Fick's Spring Manometer.

A hollow C-shaped spring (A), made of extremely thin metal, is fixed at (*b b*) where its cavity communicates with the tube (K). The top of the C is connected at (*a*) with the writing lever. Any increase of pressure in the tube (K) causes the spring to expand and move the writing point (G) up and down.

movements and consequent pressure changes within the thorax would seem to give a simple *mechanical explanation* of the variation in pressure. But if the change occurring in the intra-thoracic pressure be examined carefully, it will be found not to correspond exactly with the so-called respiratory wave of the pressure curve in the arterial system.

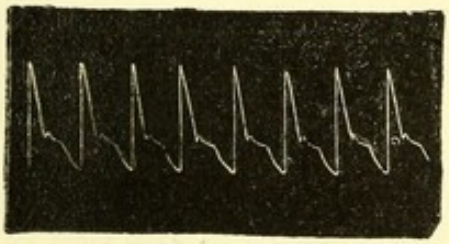


Fig. 137.—Tracing of blood-pressure taken with Fick's manometer.

The amount of pressure exercised on the pericardial contents by the lungs varies with the respiratory movements. It is slightly decreased during inspiration, and increased during expiration. The differences thus produced, however, are during ordinary respiration very slight (probably

1 mm., mercury). So slight a variation as 1 mm., mercury, cannot, by direct action on the aortic arch, cause the change of several millimetres which we see in the respiratory undulation in the arterial pressure. We must, therefore, seek the explanation in the changes it causes in the great veins.

Owing to the lungs being very elastic and constantly tending to shrink away from the costal pleura, the pressure in the pleural cavity is less than that of the atmosphere which distends the lungs, *i.e.*, the

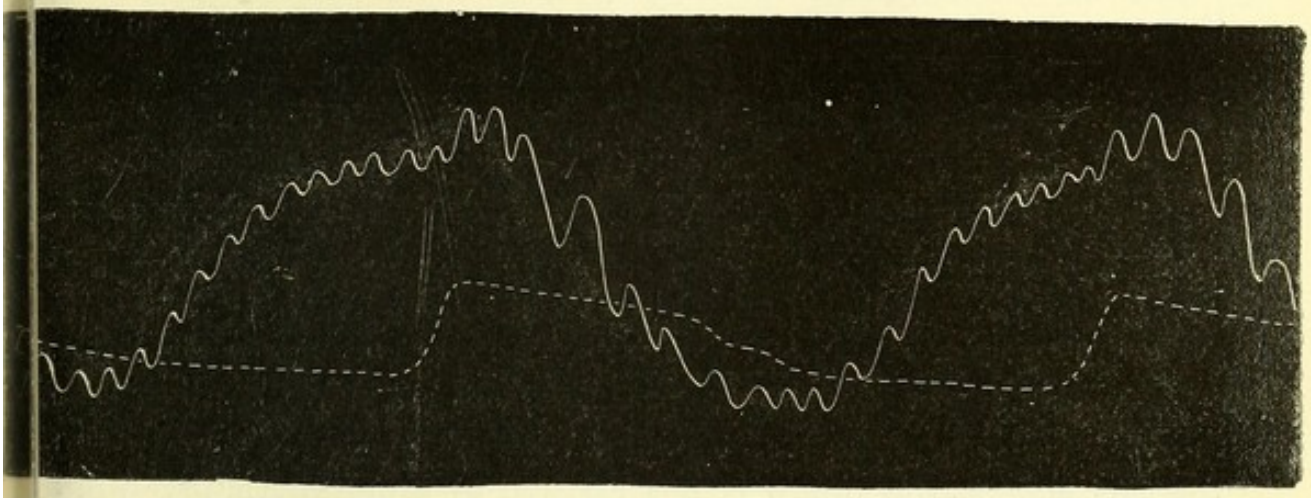


Fig. 138.—Blood-pressure and Respiratory Tracings recorded synchronously—recording surface moving from right to left—showing that the variations in pressure in the arteries (continuous line) and in the thoracic cavity (dotted line) do not exactly correspond, the latter continuing to fall after the blood-pressure has commenced to rise.

pleural pressure is *negative*. All the viscera in the thoracic cavity are habitually under the influence of the negative pressure. Thus the elastic lungs exert a kind of traction on the pericardium, and tend to cause a negative pressure within the heart and great systemic vessels, both arteries and veins. The influence is more felt by the thin-walled venæ cavæ in which the blood-pressure is low, than in the thick-walled arteries where it is high.

The flow of blood into the left auricle from the pulmonary vessels is not influenced by the negative pressure, as pressure of the atmosphere cannot reach them.

It has been suggested that by *facilitating the flow into the thorax* from the great veins, the amount of blood entering the right auricle during inspiration may be increased, and thus the left ventricles may be better filled and made to beat more actively, so as to cause an elevation in the arterial pressure.

The sequence of events may be read as follows. During inspiration the negative pressure on the right heart is increased; the atmo-

spheric pressure acting on the tributaries of the superior vena cava is unchanged, while the pressure in the abdominal cavity is increased, and the inferior vena cava compressed by the muscular action. The blood thus flows more readily into the right heart, and consequently the lungs receive a larger supply of blood during this period. In expiration, on the other hand, the intrathoracic pressure becomes less negative, the compression of the abdominal viscera is relieved, and the flow into the auricle loses somewhat in force.

But this view appears to leave the pulmonary circulation out of the question in a way hardly justifiable, since the lungs must be traversed by the blood before the increased inspiratory inflow to the right auricle can affect the left ventricle or the systemic arteries.

It must be carefully borne in mind that the *left* side of the heart works under different conditions, for the variations of pressure affect both the pulmonary veins and the left auricle similarly, since they are both included in the thoracic cavity, and are both subjected to a slightly varying negative pressure. The aid given to the flow into the right heart by the low intrathoracic pressure is quite absent on the left side, as the inflow is not assisted by atmospheric pressure ; so that the thoracic movements do not exert any influence on the flow of blood from the pulmonary veins to the systemic arteries. While inspiration is taking place the lungs receive a larger supply of blood. From the relatively large amount of blood in these organs it is probable that this slight excess has little or no influence on the amount entering the left side of the heart. The left ventricle may receive an amount of blood during expiration slightly in excess of that which it receives during inspiration. This can have but little direct effect on the pressure in the great arterial trunks.

It is more than probable that excess of blood in the heart cavities does not mechanically influence the beat or the blood-pressure, but rather acts as a nervous stimulus, and excites the inhibitory centre of the heart and the depressor centres which control the arterioles.

The rejection of this indirect mechanical explanation appears necessary from the following facts :—

(1.) The rise in pressure is not exactly synchronous with expiration or inspiration :

(2.) The heart beats more slowly during expiration than inspiration :

(3.) This difference at once disappears if the vagi be cut, and the respiratory wave becomes greatly modified :

(4.) Variations in the pressure like the respiratory wave occur after the respiratory movements have quite ceased.

(5.) The respiratory wave is observed when artificial respiration is employed, in which the forcing of air into the lungs is the *cause*, and not the *result* of the thoracic movements, so that the pressure effects are *reversed*.

We may conclude that a sympathy in action can be recognised in the working of the respiratory, vascular and cardiac nerve mechanisms.

The undulations known as Traube's Curves occurring in curarised animals when no respiratory movements are performed, have been explained by referring them to a stimulation by impure blood of the vasomotor centre, which by rhythmical impulses increases the contraction of the arterioles and causes a rhythmical variation in the blood-pressure. This explanation when applied to the respiratory waves seems to be rendered unsatisfactory by the fact that these undulations go on even when the arterioles are cut off from their chief nerve centres by sections of the spinal cord. So that if these undulations are to be referred to nerve mechanism we are ignorant of the course taken by the nerve impulses, for any rhythmical sympathy existing between the respiratory and vasomotor nerve centres in the medulla cannot well influence the vessels when the cord is cut.

Thus we seem forced to fall back upon the muscular coats of the arteries for an explanation of the respiratory variation in the blood-pressure, and to accord to this tissue automatic rhythmical contractility.

The blood-pressure in the capillaries cannot be directly measured by the means above described; it is difficult to estimate, and very variable. The slightest change of pressure in the corresponding veins or arteries causes the pressure in the capillaries to rise or fall. Thus, variations in pressure are constantly occurring in the capillaries, which cause an alteration in the rate of flow, or even a retrograde stream in some parts of the network.

The regulation of the blood-supply, and, therefore, of the pressure in the capillaries, is under the control of the small arterioles which supply them; a slight relaxation of the muscle of the arterioles causes great increase in the amount of blood flowing through the capillaries, as can readily be seen with the microscope.

The blood-pressure in the veins must be less than that in the capillaries, and, as has been said, must diminish as the heart is approached, where in the great veins (superior cava) the pressure

is said to be rather below that of the atmosphere (— 3 to — 5 mm., mercury). During inspiration the minus pressure may become further lowered, whilst, on the other hand, it is only by very forced expiration that it ever becomes equal to or at all above that of the atmosphere.

This is a most important fact, as the suction considerably helps the flow of blood from the veins, and also the current of fluid from the thoracic duct that bears the chyle from the intestines and the fluid collected from the tissue drainage back to the blood.

The pressure of the blood in the veins may be said to be generally nil, since the veins are nowhere over-filled with blood. The pressure, on the other hand, that can be registered and measured depends upon forces communicated from without, namely: (1) gravity; (2) the elastic pressure of the surrounding tissue; and (3) the pressure exerted by the muscle during contraction. This pressure is increased by any circumstance which impedes the flow of blood through the right side of the heart, through any large vein, or through the pulmonary circulation; but when no abnormal obstacle exists in the venous blood-current the pressure in those vessels can never attain any great height, for, as we have seen, the large trunks are constantly being emptied by the heart's action.

Most circumstances which tend to lower arterial pressure also tend to raise the pressure in the veins, so that, when the heart's action is weak, or its mechanism faulty, the venous pressure rises.

In the veins of the extremities the pressure greatly depends on the position of the limb, as it varies almost directly with the effect of gravity.

In the pulmonary circulation the direct measurement of the intravascular pressure is rendered extremely difficult, and possibly erroneous, by the fact that to ascertain it the thorax has to be opened. It has been found in the pulmonary artery to be in a dog 29·6 mm., in a cat 17·6 mm., and in a rabbit 12 mm. of mercury.

The Arterial Pulse.

Each systole of the ventricle sends a quantity of blood into the aorta, and thus communicates a stroke to the blood in that vessel. The incompressible fluid causes the tense arterial wall to distend still further, and the shock to the column of blood is not transmitted onward directly by the fluid, but causes the elastic walls of the arteries to yield locally, and thus it is converted into a wave which passes rapidly along those vessels. This motion in the walls of the vessel can be

felt wherever the artery can be reached by the finger, but best, as is the case in the radial and temporal arteries, where the vessel is superficial and lies on some unyielding structure such as bone.

This motion of the vessel wall is called the *arterial pulse*. It consists of a simultaneous widening and lengthening of the artery. The arteries near the heart are more affected by the pulse wave than those more remote, the wave becoming fainter and fainter as it travels along the branching arteries. In the smallest arteries it is hardly recognizable, and under ordinary circumstances is quite absent in the capillaries and veins.

The diminution in the pulse-wave in the smaller arteries chiefly depends upon the fact that the force of the wave is used up in distending the successive parts of the arteries. In the small arteries the extent of surface to which the pulse-wave is communicated is great, and thereby the wave is much decreased. It is probable that reflected waves pass from the peripheral end of the arterial tree—the contracted arterioles—and meeting the pulse-wave in the small arteries help to obliterate it. So long as the arterioles are contracted to the normal degree no pulsation is communicated to the capillaries, because the wave, reaching the arterioles, is reflected by them.

The pulse-wave can easily be shown to take some time to pass along the vessels. Near the orifice of the aorta the arterial distension occurs practically at the same time as the ventricular systole, but even with comparatively rough methods the radial pulse can be observed to be a little later than the heart-beat. The difference of time between the pulse in the facial and the dorsal artery of the foot has been estimated to be one-sixth of a second, and the difference in the distance of these vessels from the heart is about 1,500 mm., so that the rate at which the pulse-wave travels is nearly 10 metres per second. The velocity of the wave is said to depend upon the degree of elasticity of the walls of the vessels, and it would appear to be quicker in the lower than in the upper extremities.

The time that the wave takes to pass any given point must be equal to the time taken to produce it, that is to say, the time the ventricle occupies in sending a new charge of blood into the aorta, which is about one-third of a second. Knowing the rate at which the wave travels (10 m. per sec.) and the time it takes to pass any given point ($\frac{1}{3}$ sec.), its length may be calculated to be about three metres, or about twice as long as the longest artery. Thus the pulse wave reaches the most distant artery in one-sixth of a second, or about the middle of the ventricular systole, and when

the wave has passed from the arch of the aorta, its summit has just reached the arterioles.

Numerous instruments have been invented for the demonstration and graphic representation of the pulse in the human being. Of

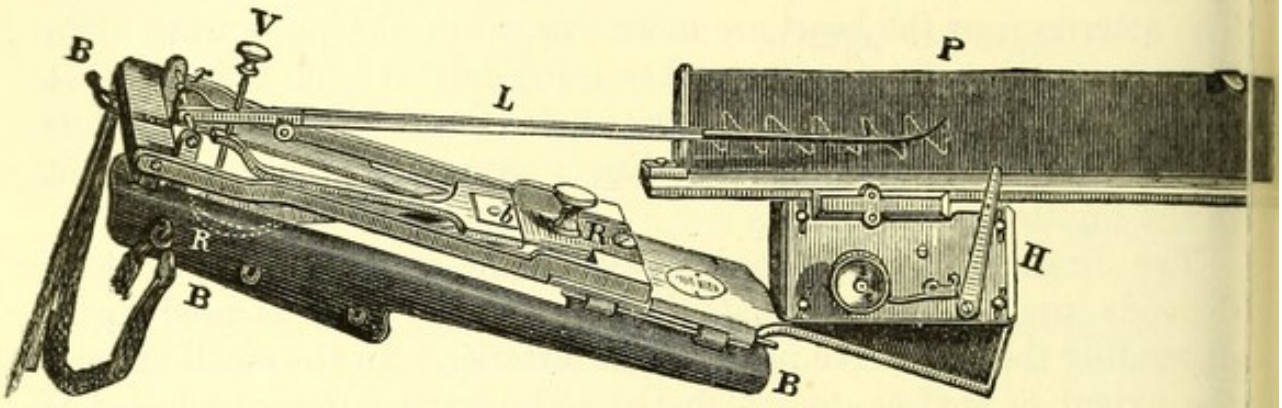


Fig. 139.—Marey's Sphygmograph.

The frame (B, B, B) is fastened to the wrist by the straps at B, B, and the rest of the instrument lies on the forearm. The end of the screw (V) rests on the spring (R), the button of which lies on the radial artery. Any motion of the button at R is communicated to V, which moves the lever (L) up and down. When in position, the blackened slip of glass (P) is made to move evenly by the clock-work (H) so that the writing point draws a record of the movements of the lever.

these the one in general use is Marey's *Sphygmograph* (Fig. 139), by means of which a graphic record of the pulse is made, in the form of a tracing of a series of elevations and depressions (Fig. 140). The elevations correspond to the onset of a wave, and the depressions to its departure, or to the temporary rise and fall of the arterial pressure. In the falling part of the curve an irregularity caused by a

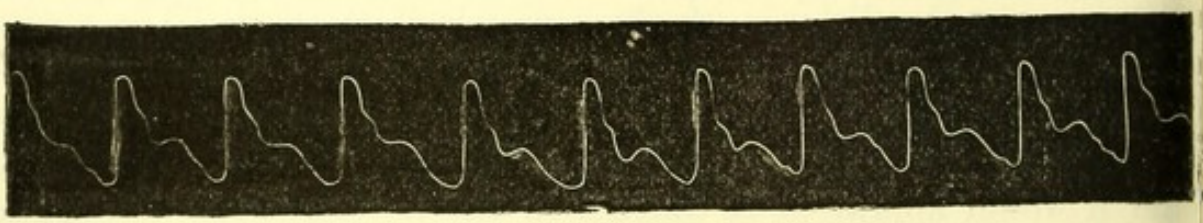


Fig. 140.—Tracing drawn by Marey's Sphygmograph. The surface moved from right to left. The vertical upstrokes show the period when the shock is given by the systole of the ventricle. The upper wave on the downstroke shows when the blood has ceased to enter the aorta. Then comes the dicrotic depression, which is a negative wave produced by the momentary backflow in aorta, and the dicrotic elevation caused by the closure of the valves.

slight second wave is nearly always seen. This is called the *dicrotic* wave. Sometimes there are more than one of these secondary waves, the most constant of which is a small wave preceding the dicrotic, called *predicrotic;* but the dicrotic is always more marked than any

other. Several waves of oscillation can be seen as a gradually decreasing series in tracings taken from elastic tubes, but we cannot say positively that they occur in the arteries. When several secondary waves exist in the pulse curve the smaller ones probably depend on oscillations caused by the lever of the instrument.

The dicrotic wave does not depend on the instrument, because in most cases the skilled finger laid on the radial artery at the wrist can easily detect it, and it can be directly seen in the vessel when the pulsation in the arteries is visible, or when a jet of blood escapes from an artery.

When a new charge of blood is shot into the aorta the elastic wall of the vessel is suddenly stretched. At the same time a shock is given to the column of blood, and the fluid next the valves is moved forwards with great velocity. Owing to its inertia the fluid tends to pass onwards from the valves, and thus allows a momentary fall in pressure which is at once followed by a slight reflux of the blood and the forcible closure of the valves.

The first crest or apex of the pulse curve corresponds to the shock given by the systole, and is greatly exaggerated by the inertia of the lever. The crest of the predicrotic wave marks the moment when the blood ceases to flow from the ventricle, and, therefore, it is the real head of the pulse wave.

The dicrotic wave has been explained as (1) a wave of oscillation, (2) a wave reflected from the periphery, or (3) a wave from the aortic valves.

(1) If the first, it should be less marked than the predicrotic, which by this theory is said to be the first wave of oscillation, for each succeeding oscillation is less than its forerunner. But, as already mentioned, the dicrotic is invariably the larger.

(2) There are many reasons why it cannot be a wave of reflection from the periphery of the arterial tree ; viz., 1. Its curve is not found to be nearer the primary wave when the peripheral vessels are approached. 2. The arterioles which form the peripheral resistance are at too irregular distances to give one definite wave of reflection. 3. It is seen in the spurting of an artery cut off from the periphery. 4. It increases with greater elasticity and low tension, which cause the reflected waves to diminish.

(3) The dicrotic notch then most probably depends upon a negative centifrugal wave, caused by the sudden stoppage of the inflow and the momentary reflux of blood during the closure of the valves ; and the dicrotic crest is, no doubt, produced by the completion of their closure, at which moment the sudden check given to the reflux of the

blood column causes a positive centrifugal wave to follow the primary wave of the pulse.

The view that the reflux of blood and the closure of the valves produce the dicrotic wave is supported by the fact that the conditions which increase the dicrotism—viz. (1) sharp strong systole, (2) low tension, and (3) perfect resiliency—promote the recoil and closure; and, on the other hand, the conditions which interfere with the closure of the valves also diminish the dicrotic wave in the most marked degree, viz. (1) inefficiency of the aortic valves, and (2) a rigid calcareous condition of the arteries.

It can be shown in an elastic tube, fitted with a suitable pump and sphygmographs, that when its outlet is closed a *positive* wave is reflected from the distal end back to the pump, and when the outlet is opened a *negative centripetal* wave is reflected. This fact assists in explaining the variations in the character of the pulse curve of the

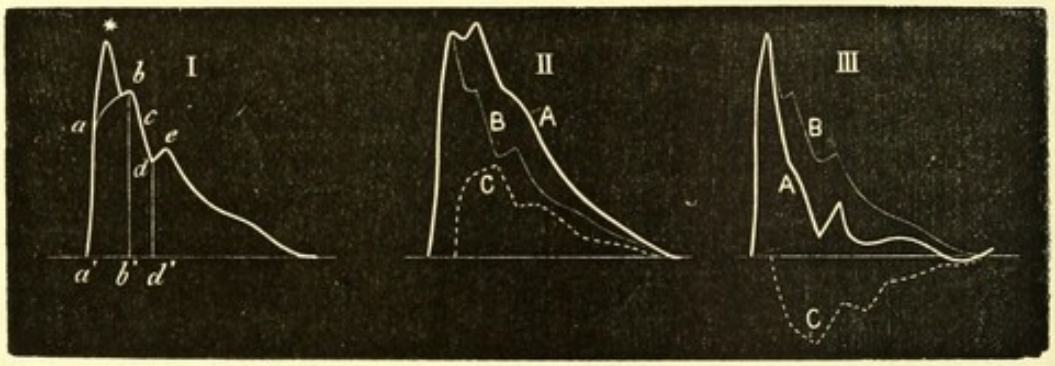


Fig. 141.

I. Scheme of Normal Pulse Curve: *a*, Entrance of ventricular stream into the aorta, the lever is jerked too high, reaching *; *ab* shows real summit of waves; *b*, point at which stream from ventricle ceases; *c*, negative wave caused by (1) sudden cessation of inflow and slight reflux of blood; *d*, point of closure of aortic valves; *e*, positive wave from valves (dicrotic wave). The time may be measured on abscissa at *a' b' d'*.

II. Scheme of High Tension Pulse Curve; (constricted arterioles). A. Curve of radial pulse, which is the resultant of *positive* reflected wave c added to the primary curve B.

III. Scheme of Low Tension Pulse Curve; (dilated arterioles). A. Radial pulse curve, which is the resultant of the *negative* reflected wave c subtracted from the primary wave B. (After Grashey.)

radial artery where the equidistance of the derived arterioles enables the reflected waves to have considerable effect. When the arterioles are constricted (a condition corresponding to the closure of tube) a positive centripetal wave is reflected and is *added* to the pulse-wave so as to diminish the dicrotic notch, and give the curve known as characteristic of the "high tension" pulse, seen in Bright's disease. (Fig. 141, II.) On the other hand, when the arterioles are widely dilated (corresponding to the open condition of the tube) a

negative wave is reflected, and is *subtracted* from the force of the pulse-wave so as to exaggerate the dicrotic notch, and give the tracing characteristic of the "low tension" pulse seen in fever, &c. (Fig. 141, III.)

The mean rate of the pulse varies in different individuals, seventy-two per minute being a fair average for a middle-aged adult. It varies also with many circumstances, which though purely physiological must be borne in mind in taking the pulse as a clinical guide.

1. *Age.* At birth it is about 140 per minute, and is, generally speaking, quicker in young than in old people, commonly falling to 60 in aged persons.
2. *Sex.* It is more rapid in females than in males.
3. *Posture.* It is quicker standing than lying, particularly if a patient who has been lying down, stand or sit up, the pulse becomes more rapid.
4. *The time of day.* At its minimum at midnight, it gains in rapidity till 9 o'clock in the morning; falls in the day-time, and rises in the evening till 6 o'clock.
5. Muscular exercise quickens it.
6. It is quicker during inspiration than expiration.
7. It increases with increase of temperature.
8. It is variously affected by emotions.

Velocity of the Blood Current.

The velocity of the blood must not be confounded with the velocity of the pulse wave, which bears to it the same relation as the surface waves on a river do to the rate of the stream of water.

It has already been mentioned that the general bed of the blood increases from the aorta to the capillaries, and decreases from the capillaries to the vena cava. The branches or tributaries of an artery or vein have collectively a larger sectional area than the vessel from which they spring or to which they lead respectively; or, in other words, if we imagined the whole vascular system fused together into one tube it would form two somewhat irregular cones, one corresponding to the arteries and the other to the veins, with their bases placed at the capillaries and their apices at the heart. Between the two cones a still wider portion would represent the aggregate sectional area of the capillaries. Fig. 128, p. 238.

Since the same quantity of blood must pass through each section of these cones in a given time, the rate at which it flows must vary greatly in the different parts, being faster in proportion as the

diameter of the part is narrower, in accordance with the well-known physical law that with the same *quantity* of liquid flowing, its *velocity* changes inversely with the square of the *diameter* of the tube $\left(V \propto \frac{q}{d^2}\right)$. Thus, the mean velocity of the flow in the arteries becomes slower as the capillaries are approached, and in the wide bed of the latter the rate of the current is reduced to a minimum. In the small veins the rate is slower than in the larger trunks, but on the venous side its rapidity never reaches that of the aorta, where it may be said to move at least twice as quickly as in the vena cava.

The following table may be useful in giving a general idea of the average velocity in different parts of the circulation :—

Near valves of aorta—while the ventricles are contracting it reaches	1200 mm. per sec.
Descending aorta	300—600
Carotid	205—357
Radial	100 mm. per sec.
Metatarsal	57 „
Arterioles	50 „
Capillaries	0·5 „
Venous radicles	25 „
Small veins on dorsum of hand	50 „
Venæ Cavæ	200 „

In the aorta near the valves the blood current varies in rapidity, because the flow through the aortic orifice is intermittent, and this variation must be more or less communicated to the neighbouring arteries in the form of an increase of rapidity coincident with the beat of the arterial pulse. The variation in the rate of the blood-flow which is caused by the heart-beat, diminishes with the force of the pulse as the smaller arteries are approached, and finally ceases completely in the capillaries where under ordinary circumstances the flow is perfectly continuous. In the first part of the aorta the velocity of the blood-flow is reduced to nil after each ventricular beat, while in the capillaries no change is perceived. Between these two extremes all gradations may be found, which follow the same rules as the pulse.

The general mean velocity varies directly with the blood-pressure, which bears a generally inverse relation to the calibre of the arteries. The velocity in any one artery, and its branches, will vary with the calibre of those vessels, which are constantly undergoing local changes in size.

Generally speaking, quick heart-beats cause increase in velocity of the stream, but no definite or invariable relation exists between the rate of the heart-beat and the current of the blood. The vaso-motor influences have, no doubt, much more effect than the heart-beat on the rate of the stream in the smaller vessels the calibre of which they control.

In looking at the blood passing through the small vessels of a transparent tissue, such as the frog's tongue or web, it appears that different parts of the column of fluid move with different velocities. Down the centre of the stream the red corpuscles are seen coursing rapidly, while between the central part and the vessel wall on each side a pale line of plasma can be recognised, which seems to flow more slowly and to carry with it only a few white corpuscles.

In the veins the velocity varies greatly with a variety of circumstances which have little or no effect on the arterial flow. Thus, the position of the body or limb, the activity of the neighbouring muscles and the respiratory movements alter it, but as a general rule the flow in the veins is pretty steady, there being no pulsation or corresponding variation of velocity. In the large vessels the onward flow is affected by the contraction of the auricles. During the auricular systole the veins cannot empty themselves, and therefore there is a slight check to the onward flow, and the velocity of the current is correspondingly reduced. In cases where the auricles are dilated and distended with blood this may cause a definite pulsation, which becomes visible in the great veins of the neck.

Work done by the Heart.

The amount of work done by any form of engine may be expressed as so many kilogrammetres per hour. That is to say, the numbers of kilogrammes it could raise to the height of one metre in that time.

The left ventricle moves with each systole about 0·188 (Volkman) kilogrammes of fluid against an arterial pressure corresponding to 3·21 (Donders) metres height of blood, *i.e.*, $0{\cdot}188 \times 3{\cdot}21 = 0{\cdot}604$ kilogrammetres for each systole. This at 75 per minute for 24 hours would be—

$$0{\cdot}604 \times 75 \times 60 \times 24 = 65{,}230 \text{ kilogrammetres.}$$

The right ventricle does about one-third as much work as the left, making a total of 86,970 kilogrammetres for the ventricles. Or, in other words, the heart of a man weighing twelve stone does as much

work in twenty-four hours as would be required to lift his body 1248 yards into the air, *i.e.*, nearly ten times as high as the steeple of St. Paul's Cathedral.

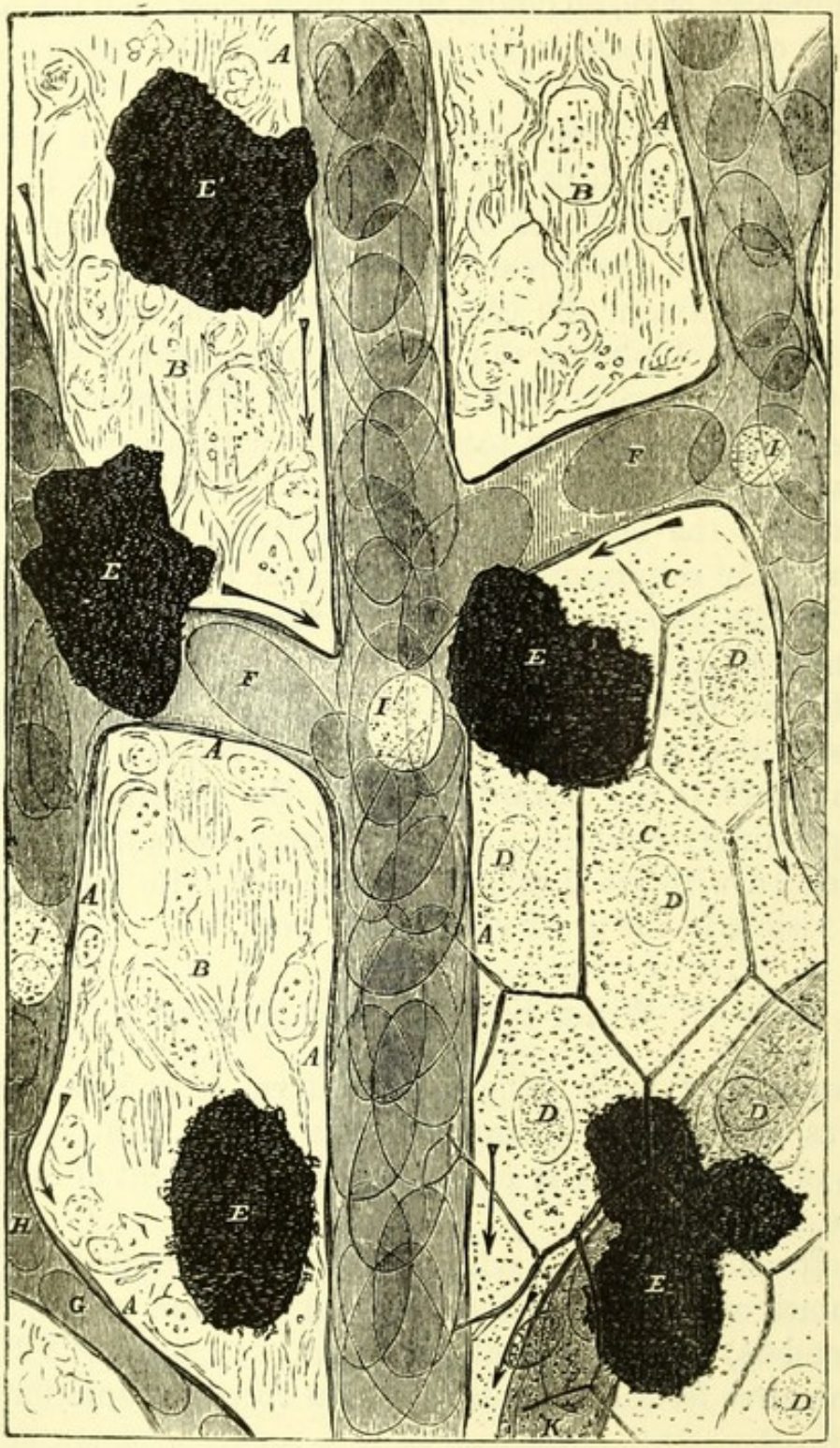


Fig. 142.—Small portion of Frog's Web, very highly magnified. (Huxley.)

A. Wall of capillary vessels.
B. Tissue lying between the capillaries.
C. Epithelial cells of skin, only shown in part of specimen where the surface is in focus.
D. Nuclei of epithelial cells.
E. Pigment cells contracted.
F. Red corpuscles (oval in the frog).
G. H. Red corpuscles squeezing their way through a narrow capillary, showing their elasticity.
I. White blood cells.

Controlling Mechanisms of the Blood-Vessels.

Vaso-Motor Nerves.

That the arteries possessed elastic resiliency and vital *contractility* which regulated the amount of blood flowing to any given part was observed by John Hunter in studying inflammation.

The muscle cells have long since been clearly demonstrated in the middle coats of the arteries, but nothing was known of the nervous channels which bore the stimulus to the vessels, or the nerve centres which regulated their contraction, until comparatively recent times.

The first definite knowledge concerning special nerves for the control of the muscular wall of the vessels is due to Claude Bernard. He showed that cutting the sympathetic nerve in the neck, was followed by an increase in temperature of that side of the head, and a great dilatation of the arteries.

It was further observed that stimulation of the superior ganglion of the sympathetic brought about an opposite result, namely, a fall in temperature and contraction of the vessels on the side at which the stimulus was applied. If the stimulus was increased, the vessels contracted more than the normal, but on cessation of the stimulus they became dilated above the normal and the temperature again rose ; the effects of the stimulus gradually passed off. From this it was concluded that the sympathetic in the neck contained *constrictor fibres* which conveyed impulses causing habitual *tonic contraction* of the vessel wall, corresponding to what was already recognised as *arterial tone.* On section of the nerve the tonic contraction disappeared, but on gentle stimulation it reappeared, and if more strongly stimulated an excessive contraction set in causing occlusion of many of the vessels.

Subsequent experiments have shown that all the vessels are supplied with similar vaso-motor (constrictor) nerves, section of which causes dilatation, while stimulation causes contraction of the vessels in the territory presided over by the stimulated nerve.

It has also been shown that the vaso-constrictor nerves for all parts of the body come from the cerebro-spinal axis, passing out from the spinal cord as extremely fine medullated fibres (white rami communicantes) by the anterior roots of all the spinal nerves between the 2nd thoracic and 2nd lumbar. They join the sympathetic, which may be regarded as a chain of vaso-motor ganglia, and are distributed to the vessels either as special nerves, branches of the

sympathetic, as the splanchnics, or with the general peripheral nerve trunks.

Although stimulation of almost any nerve causes vascular contraction, it has been shown that in some parts stimulation gives rise to an opposite result, viz., vascular dilatation. Thus, stimulation of the chorda tympani or nervi erigentes is followed by dilatation of the arterioles of the submaxillary gland and penis respectively. This dilatation is caused by the nerve-impulses checking the normal contraction by inhibiting the activity of the vascular muscles. It is believed that all arterioles may be influenced by such fibres, but the greater power of the constrictor fibres in most nerves prevents their demonstration.

These *vaso-dilator* fibres also come from the central nervous system, but leave it by routes quite different from those traversed by the vaso-constrictor fibres, and are not connected with the sympathetic ganglia. They pass out above by the vagus and glosso-pharyngeal nerves and below with the lower sacral nerves. No vaso-inhibitory fibres have been found to pass by the other spinal roots.

Vaso-motor Centres.

The nerve cells which govern the majority of the vaso-motor channels, lie in the upper part of the medulla oblongata in the floor of the fourth ventricle. This is proved by two facts : 1st, most of the brain may be removed without diminishing the arterial tone ; and 2nd, if the spinal cord be cut below the medulla (artificial respiration of course being kept up) the mean blood-pressure is found to fall immediately, almost to the level of the atmospheric pressure, owing to the relaxation of the smaller arteries consequent on the paralysis of their muscular coat.

The changes in the capillary circulation caused by vascular paralysis can be seen in the web of a frog, in which the medulla has been destroyed (pithed) while the circulation is being studied. The small arteries dilate and the pulse becomes apparent in the capillaries, and even in the veins.

It seems probable that in the medulla oblongata a *vaso-motor centre* exists, which can regulate the contraction of all the vessels, and keep them constantly more or less contracted. This slight general vascular constriction is spoken of as the arterial tone. The existence of such a centre in the medulla, and of nerve channels in the cord leading from it is made certain by the fact that if a gentle stimulus be applied to a certain part of the medulla, or just below it, simul-

taneous general vascular constriction sets in as indicated by a great and sudden rise in the blood-pressure.

Pressor Influences.—The action of the vaso-motor centre can be increased, the tone of the vessels elevated, and the pressure raised, either by (1) direct or (2) reflex excitation. *Directly*, if the blood flowing through the medulla contains too little oxygen or too much waste products it stimulates the centre and the blood pressure rises.

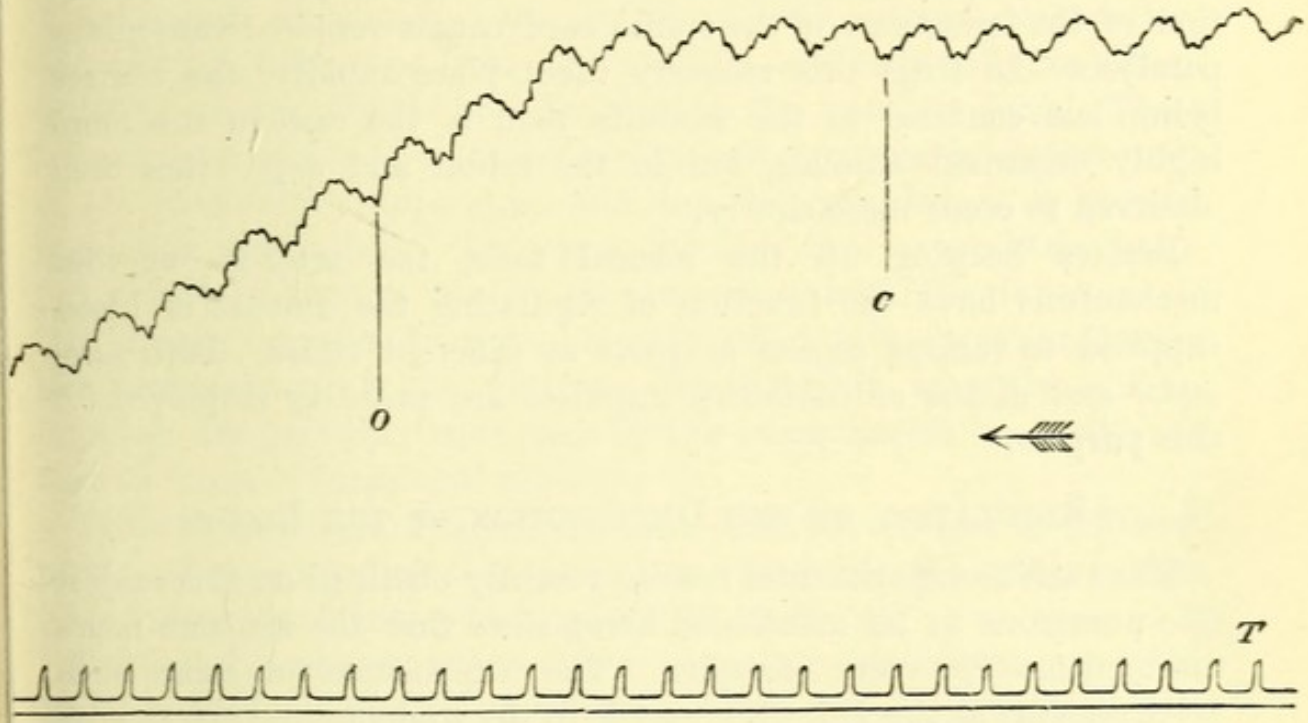


Fig. 143.—Kymographic tracing showing the effect on the blood-pressure curve of stimulating the central end of the depressor nerve in the rabbit. The recording surface moving from left to right. (c) Commencement and (o) cessation of stimulation. There is considerable delay (latency) in both the production and cessation of the effect. (T) Marks the rate at which the recording surface moves, and the line below is the base line. (Foster.)

This may be seen by temporarily suspending artificial respiration during an experiment on blood pressure, when the pressure rises considerably. *Reflexly* the activity of the vaso-motor centre can be increased by (1) the stimulation of any large sensory nerve, or (2) by sudden emotion (*fear*).

Depressor Influences.—The tone of the arteries may be diminished by inhibiting the activity of the vaso-motor centre by the stimulation of a certain afferent nerve, the anatomy of which has been made out in the rabbit, and some other animals, and probably has its analogue in man. It passes from the inner surface of the heart to the vaso-motor centre in the medulla. The effect of stimulation of this nerve in lowering the blood-pressure is so great that it is called the *depressor nerve.*

Some emotions (*shame*) may also reduce the activity of the centre, as seen in blushing, which is simply dilatation of the facial vessels.

Subsidiary Centres.—Besides this chief vaso-motor centre it is probable that in the higher animals, as certainly is the case in the frog, other centres are distributed throughout the spinal cord which are able to take the place of the great primary centre. After the spinal cord has been cut high up, the hinder extremities more or less recover their vaso-motor power in a few days, and destruction of the lower part of the spinal cord causes renewed vaso-motor paralysis. In frogs this recovery takes place rapidly, the centres being less confined to the medulla than is the case in the more highly organised animals, but in the rabbit and dog it has been observed to occur more slowly.

Besides keeping up the normal tone, the arterial nervous mechanisms have the function of regulating the amount of blood supplied to various organs or parts at different times. Both *vaso-motor* and *dilator* or *inhibitory* impulses are probably employed for this purpose.

Regulation of the Distribution of the Blood.

The various experimental results recently obtained on this subject (too numerous to be mentioned here), show that the vascular nerve mechanisms are very complex. The supposition of some such arrangements as the following may help the student.

1. The blood-vessels have muscular elements which, though commonly controlled by nerves, are capable of automatic activity. A supply of arterial blood is sufficient stimulus for their moderate action, and mechanical or other local stimulus is capable of exciting increased constriction. We know that such automatic contractile elements exist in some of the lower animals (snail's heart, hydra, &c.), and we have no reason to doubt their existence in mammals. Moreover, such a view obviates the necessity of supposing that local nerve elements exist, which cannot be recognised morphologically.

2. In the medulla oblongata there exist nerve cells which exert a constant influence over the activity of the vascular muscles. These groups of nerve cells which compose the *vascular nerve centres* may be divided into *motor* and *inhibitory*. From these centres impulses of two distinct kinds emanate, the one increasing the action of the contractile elements, and the other diminishing it. They are intimately connected with the centres which preside over the functional activity of the various viscera, and are also closely related to the nerves coming from all parts of the circulatory apparatus.

3. Direct communication between these *vaso-motor* and *vaso-inhibitory* centres and the blood-vessels is kept up by means of efferent nerve-channels, some bearing stimulating (vaso-constrictor) others inhibitory (vaso-dilator) impulses.

4. The activity of the contractile elements of any given vascular area may be altered by influences from different sources. (α.) Local influences are brought but little into play, but, if the part be cut off from the nervous centres, they are capable of controlling the local blood supply by changing the degree of local arterial constriction. (β.) Central influences from the medulla, are habitually in action, affecting all the vessels and keeping up the vascular tone. These impulses are variously modified by changes occurring in distant parts of the circulatory apparatus, and can be regarded as a general regulating mechanism. They pass through the sympathetic chain. (γ.) Special influences, which are associated with the functions of the different parts and organs, are only called into operation during the performance of the function, whatever it may be. These impulses are probably conveyed by the same nerves as excite the various forms of functional activity.

These three modes of regulation have different powers in different parts, and thus we find that section or stimulation of certain nerves gives vaso-motor effects which appear contradictory.

Section of a sensory nerve causes temporary vaso-motor paralysis, owing to the tonic constrictor influence being cut off. Stimulation of the peripheral stump causes vaso-constriction from excitation of the fibres bearing these impulses.

The stimulation of a motor nerve causes an increase in the flow of blood through the muscle, *i.e.*, is associated with a vaso-dilator effect, probably dependent on the inhibitory influence of certain efferent fibres which check the local vascular agencies.

Thus we must suppose that there exist local agents under the control of the medullary centres, and that there are distinct sets of efferent, exciting and inhibitory, fibres passing between the centre and periphery. One set of fibres lies in the ordinary functional nerve of the part, the other in the sympathetic, which to a great extent runs along the vessels themselves, and forms intricate networks.

As far as we know anatomically there are no local agents other than the muscles in the wall of the vessels. Since the impulses from the centres which can stimulate or inhibit the activity of the local agents travel by different fibres, all the observed phenomena may be explained without supposing local nerve centres to exist.

CHAPTER XVIII.

THE MECHANISM OF RESPIRATION.

The blood undergoes a series of modifications, and is constantly being altered as it passes from one part or organ to another.

It has already been seen that a quantity of nutrient material is taken up by the blood on its way through the capillaries of the alimentary tract, and a stream of lymph and chyle is poured into it when it reaches the great venous trunks; so that from two sources the blood is obviously increased in quantity. The most essential change that takes place in the circulatory fluid is the respiratory, and the addition it most urgently demands is that which it receives in the capillaries of the lungs. All the blood passes through these organs, in order to ensure the elimination of the carbonic acid acquired in the general systemic capillaries, and the re-charging of the red corpuscles with oxygen.

These gas interchanges will form the subject-matter of the present chapter; and the more especial modifications which the blood undergoes in the ductless glands, the spleen, the liver, &c., as well as in the kidneys and other excretory glands, will be considered subsequently.

As has already been pointed out (Chapter V.), an animal during its life may be said to use the substances supplied to it in food as fuel, and thus to acquire the energy which is bound up in them; for the activities of the various tissues are really combustions, being invariably associated with an oxidisation of some of the carbon compounds, so as to produce carbon dioxide and water. In order that the structures may be able to undergo this change they must have a ready supply of oxygen constantly at hand, and, moreover, the carbon dioxide which is formed in the process must be removed. The regular income of oxygen and the regular discharge of carbon dioxide are the first essentials to life; hence we find in almost all animals special arrangements known as the respiratory apparatus, by

means of which these gases can find their way to and from the tissues and external air respectively.

Here, as in the case of the nutritive materials, the blood acts as the carrier. The pulmonary half of the circulation is devoted to the gas interchange between the blood and the atmosphere, and is sometimes spoken of as *external respiration.* The gas interchange between the blood and the tissues takes place in the general systemic capillaries, and has, therefore, been spoken of as the *internal* or *tissue respiration.*

In mammalia the pulmonary apparatus is so far perfected that all the necessary gas interchange can be carried on by the lungs, and the respiratory influence of the external skin or the mucous passages may be regarded as insignificant. But it should be remembered that, whenever the blood is in close relation to oxygen, as in the case of swallowed air, the oxygen is soon absorbed by the blood.

In some of the lower animals the cutaneous surface aids very materially in respiration; for example, frogs can live by this cutaneous respiration alone for an almost indefinite time.

The change in the lungs consists in (1) oxygen being taken from the atmospheric air * by the blood and (2) carbon dioxide being given off from the blood to the air. In the capillaries, on the other hand, the blood takes the carbon dioxide from the tissues, and yields to them a great portion of its oxygen.

Respiratory Mechanism in Lower Animals.

In the lowest class of animals (*e.g.*, amœba), we find no special organs for the purpose of respiration, the gas interchange being sufficiently provided for by the exposure of the general surface of their bodies to the medium in which they live, namely, water.

All higher animals have some special apparatus for the purpose of respiration. This apparatus has always the same essential object, that of exposing their tissues to a medium containing oxygen, and of removing the carbonic acid gas.

In some of the invertebrate animals it suffices to distribute the medium containing oxygen throughout the tissues of the animal by means of tubes. Thus in the Echinodermata a water vascular system

* The composition of the atmosphere is everywhere remarkably constant, in spite of its oxygen being used up by living beings. It consists of—

Oxygen	21 vols. per cent.
Nitrogen	79 ,, ,,
Carbonic acid gas (variable)	·04 ,, ,,
Moisture (variable)	8 ,, ,,

exists which seems to carry on the function of respiration. A somewhat similar method of distribution of oxygen takes place in arthropoda, in which delicately branching open tubes (tracheæ) distribute air to the tissues of the animal's body.

When more active changes occur in the tissues there is always a perfect blood vascular system. The blood is invariably used as the distributing and collecting agent of the gases in the tissues, and by flowing through some special organ exposed to the surrounding medium it ensures the gas-interchange between the body and the outer world. These organs are formed on two general types: (1) external vascular fringes; and (2) internal vascular sacs.

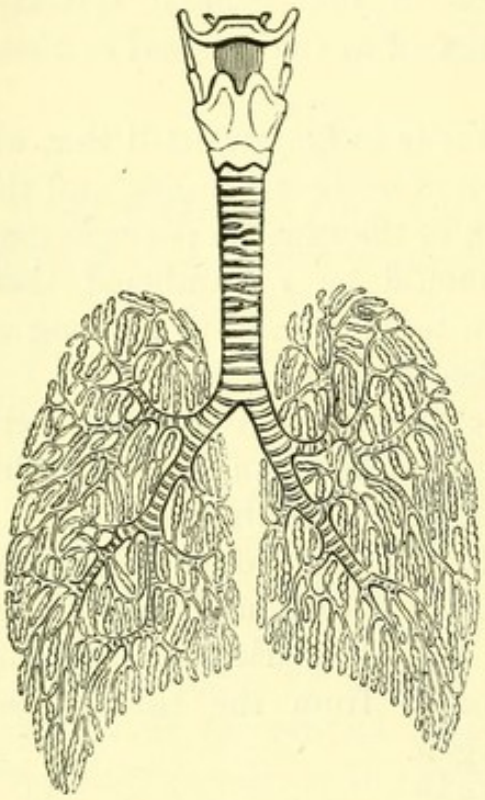


Fig. 144.—Diagram of the Respiratory Organs. The windpipe leading down from the larynx is seen to branch into two large bronchi, which subdivide after they enter their respective lungs.

Animals living in water have commonly the external fringe arrangement (gills) whilst those living in air have sacs (lungs). Some animals (frogs, toads, &c.) have gills in the early stages of their life, and lungs when they are more fully developed. In frogs and serpents the lungs are simple sacs, with the inner surface increased by folds of the lining membrane, which gives it a honeycomb appearance; into each sac opens one of the divisions of the air-tube. In crocodiles the air-tubes divide into several branches which open into a series of anfractuous vascular recesses communicating one with another.

In birds wide bronchial tubes pass through the lung tissue to reach large air cavities. The walls of the tubes are studded with the openings of innumerable air-cells lined with capillary blood-vessels. The terminal air cavities are not vascular as in the mammalian lung.

Structure of the Lung and Air Passages.

The respiratory apparatus of mammals consists of (1) vascular sacs filled with air, known as the lung alveoli; (2) channels by which

these sacs are ventilated—the air passages ; (3) motor arrangements, which carry on the ventilation of the lungs—the thorax.

1. The *lungs* are made up of innumerable minute cavities (alveoli), with thin septa springing from the inner surface so as to divide the space into several compartments or air-cells. Each of these cavities forms a dilatation on the terminal twig of a branching bronchus, and may be regarded as an elementary lung. The aggregate of these cavities, and the branches of the air passages and vessels distributed to them make up the structure of the lung.

The walls of the cavities are formed chiefly of fine elastic fibres, and the surface is lined with exceptionally delicate and thin celled epithelium. Supported in the delicate framework of elastic and connective tissue is the remarkably close-set network of capillaries, in which the blood is exposed to the air. The delicate wall of the vessel, and the thin body of the epithelial lining cell are the only structures interposed between the blood and the air.

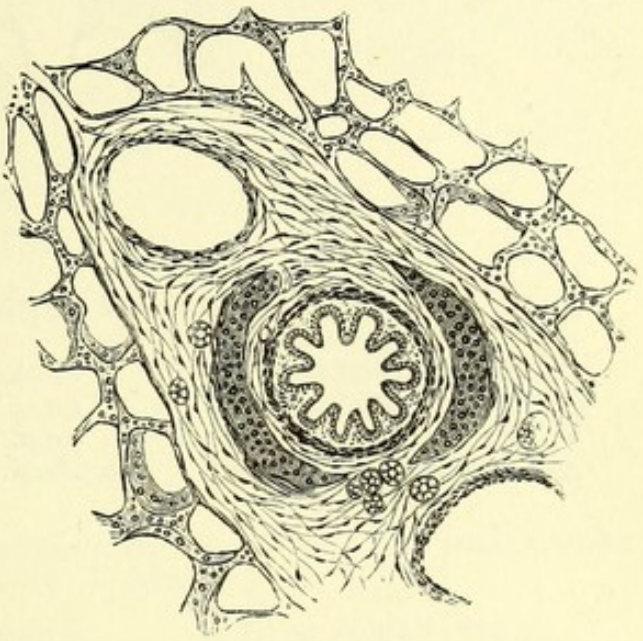


Fig. 145.—Section of small portion of Lung in which are seen a bronchial tube with its plicated lining mucous membrane in the centre, and the large blood-vessels at the sides cut across. Loose areolar tissue and numerous lymphatics surround the large vessels and separate them from the lung tissue.

Pleura. — The external surface of the lungs is invested by a serous membrane—the pleura, which is reflected to the wall of the thorax from the roots of the lungs, and completely lines the cavity in which they lie. Thus the lungs are only attached to the thorax where the air passages and great vessels enter, the rest of their surface being able to move over the inner surface of the thorax, and to retract from the chest wall if air be admitted into the pleural sac.

2. The *air passages* are kept permanently open during ordinary breathing by the elasticity of their tissues. The trachea and bronchi have special catilaginous springs for the purpose. These are closely attached to the fibro-elastic tissues which complete the general foundation of the walls of the tubes. The air passages are through-

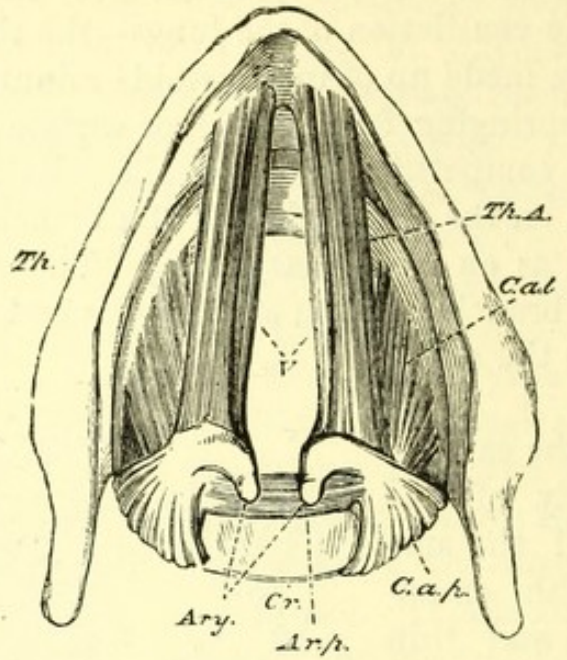


Fig. 146.—Muscles of Larynx, viewed from above.

Th. Thyroid cartilage.
Cr. Cricoid cartilage.
V. Edges of the vocal cords.
Ary. Arytenoid cartilages.
Th.A. Thyro-arytenoid muscle.
c.a.l. Lateral crico-arytenoid muscle.
c.a.p. Posterior crico-arytenoid muscle.
Ar. p. Posterior arytenoid muscle.

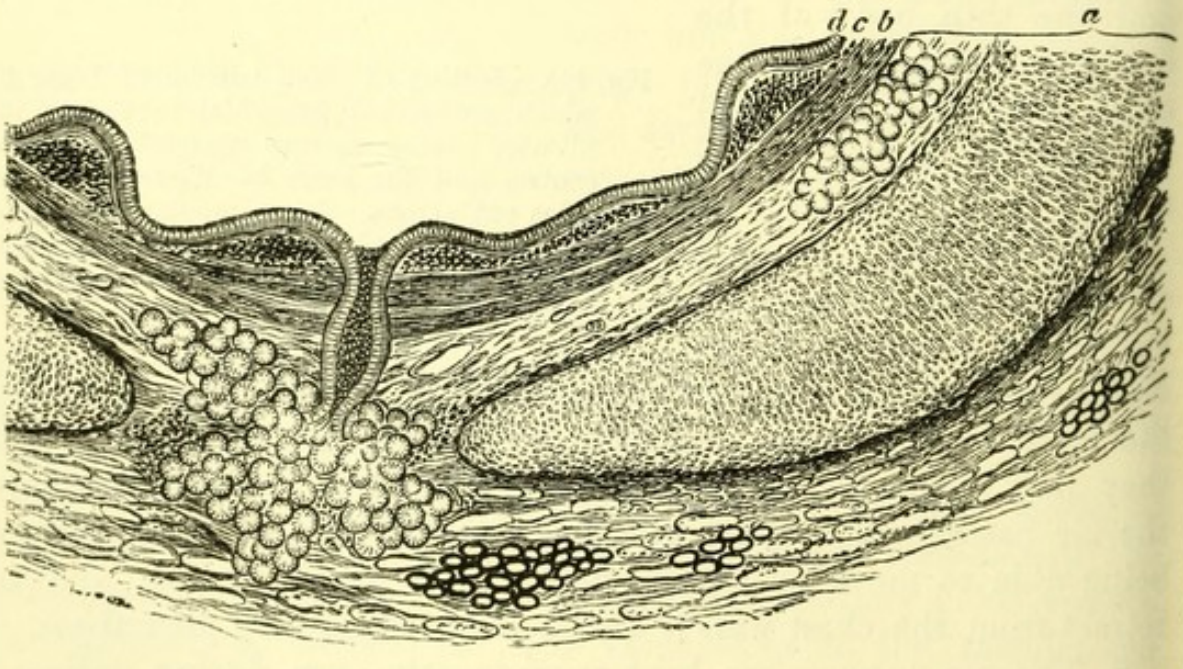


Fig. 147.—Transverse section of part of the wall of a medium-sized bronchial tube. × 30. (F. E. Schultze.)

a. Fibrous layer containing plates of cartilage, glands, &c.
b. Coat composed of unstriated muscle. *c*. Elastic sub-epithelial layer.
d. Columnar ciliated epithelium.

out lined with ciliated columnar epithelium, which, at the entrance to the infundibula, loses its cilia, and is converted into a single layer of flattened cells.

The air-passages are supplied with muscle-tissue of different kinds.

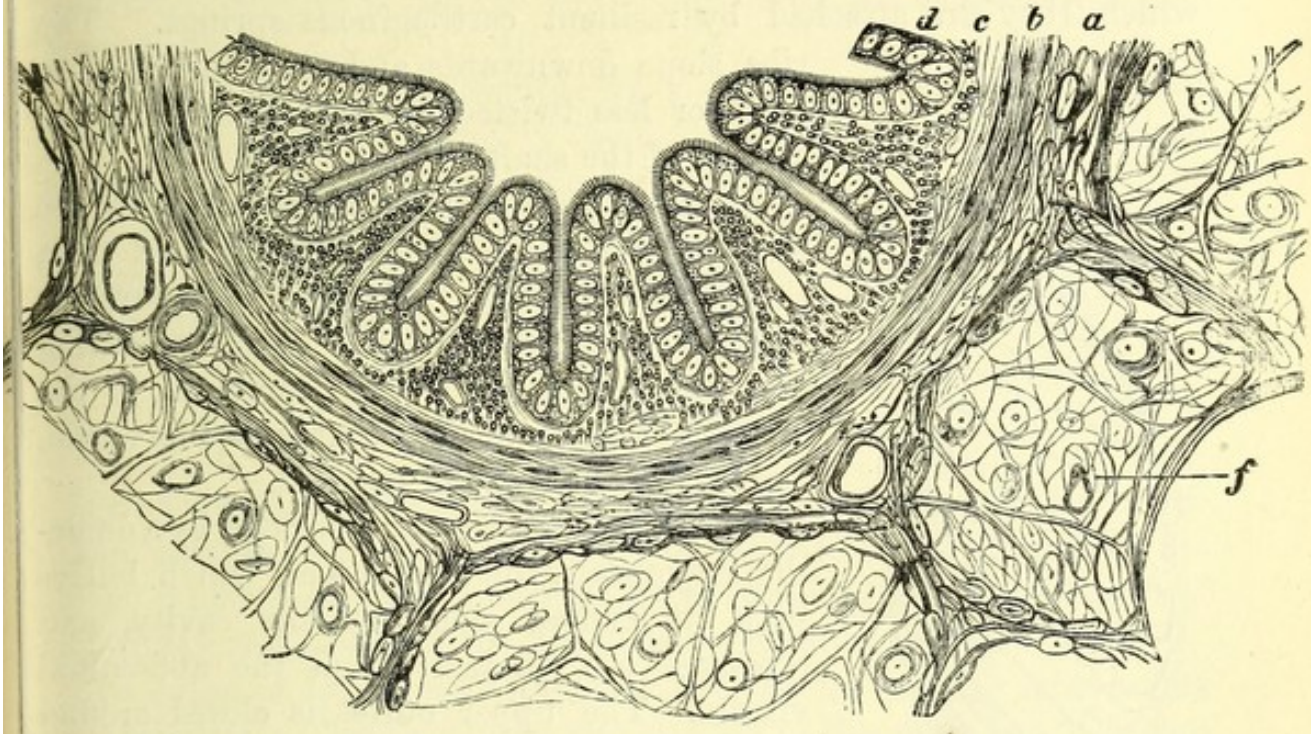


Fig. 148.—Section of a portion of Lung Tissue, showing part of a very small bronchu cut across. (F. E. Schultze.)

a. Fibrous layer containing blood-vessels.
b. Layer of unstriated muscle.
c. Layer of elastic fibres.
d. Ciliated epithelium.

Besides the ordinary striated muscles that control the opening of the anterior and posterior nares and pharynx, a special set surrounds the upper part of the larynx, and is capable of completely closing the glottis, and thus shutting off the lung cavities, and proper air-passages from the outer air. (Fig. 146.)

In the trachea a special muscle exists which can narrow the wind-pipe by approximating the extremities of the C-shaped springs that normally preserve its patency.

In the bronchial tubes a large quantity of smooth muscle-cells exist, for the most part arranged as a circular coat, which is best developed in the small tubes (fig. 148, *b*). As we pass from the large to the smaller bronchi the walls become thinner and less rigid, and the cartilaginous plates and fibrous tissue gradually diminish, while on the other hand the muscular and elastic elements become relatively more abundant.

3. The *thorax*, in which the lungs are placed, is a bony framework,

the dimensions of which can be altered by the muscles which close in and complete the cavity.

The framework is a rounded blunt cone composed of a set of bony hoops, the ribs, attached by joints to a bent pliable pillar, the vertebral column, and held together in front by the sternum, to which they are attached by resilient cartilaginous springs. The ribs slope downwards and forwards, and are more or less twisted on themselves about the middle of the shaft.

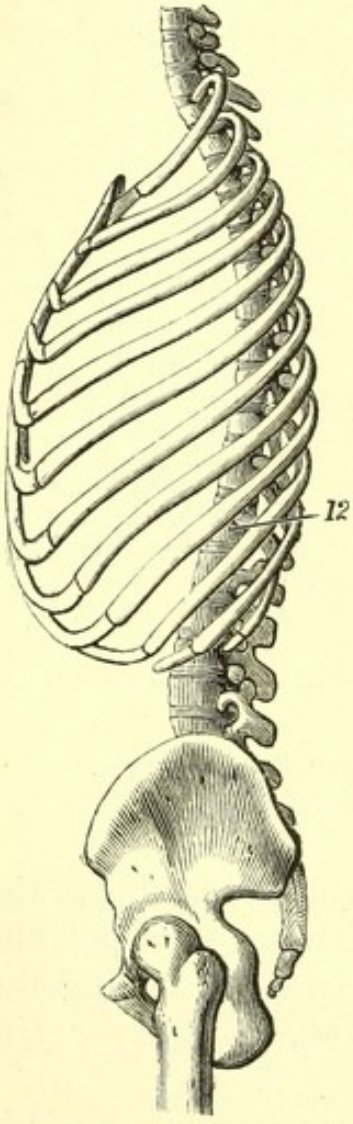


Fig. 149.—Drawing of the lateral view of Thorax in the position of gentle inspiration, showing the downward slope of the ribs.

The first pair of ribs, which encircles the apex of the thoracic cone, forms part of a short flattened hoop. It slopes downwards in front to reach the sternum. Each succeeding rib from above downwards increases in the amount of its slope downwards and forwards, and in the obliquity of its shaft.

The floor of the thorax is formed by a dome-shaped muscle, the diaphragm, which bulges with its convex side into the cavity, and separates the thoracic from the abdominal viscera. The upper outlet is closed around the trachea by several muscles, which pass obliquely upwards from the upper part of the thorax to the cervical vertebræ, and hold that part of the chest in position. These muscles can elevate as well as fix the first rib, as will be seen when speaking of the muscles in detail. The intervals between the ribs are filled up by two sets of muscular fibres, which cross one another at right angles, and are attached to the margins of the neighbouring ribs.

The base of the thorax is connected by a number of strong muscles with the pelvis and the spine, whence they pass upwards to the lower ribs. The anterior muscles pull down the sternum and anterior part of the ribs. The posterior fix and extend the last rib.

From a mechanical point of view the thorax may be regarded as a specially arranged bellows, the dimensions of which can be increased in all directions.

Within this bellows are the lungs, which may be regarded as an

elastic bag, the interior of which communicates with the outer air by an air-pipe, the only way by which the atmosphere can reach the interior of the bellows. When the framework enlarges, the pressure of the atmosphere forces a stream of air into the elastic sac, so as to distend it, and thus fill the space caused by the expansion of the framework.

By the motions of the framework a stream of air passes in or out of the sac ; a small quantity of the air in the bronchi is thus changed at each breath, and a certain standard of purity kept up.

In order to fully understand the motions by which the thorax is enlarged, a more detailed knowledge of the anatomy of the bony case and its muscles than can be given here must be acquired.

Respiratory Movements.

Physiologically the motions are divided into two sets—(1) those which enlarge the thoracic cavity, and cause the air to rush into the lungs, called *inspiration ;* and (2), those which diminish the size of the thorax and force out the air, called *expiration.*

No action of life is more familiar than the rhythmical movements of respiration. The slow quiet rise and fall of the chest and abdomen are the signs most commonly sought as indicative of life ; for every one knows that constant ventilation must go on in order that the blood may readily obtain the necessary amount of oxygen, and get rid of carbonic acid gas, the ordinary diffusion that takes place in the motionless chest being quite insufficient to remove the heavy carbonic acid gas from the lungs.

The rhythm of the respiratory movements may be represented graphically by recording the changes in the diameter or circumference of the thorax, the movements of the diaphragm, or the variations of the pressure in the air-passages. These methods, though not quite reliable, give curves of a similar character.

The rate of the respiratory movements is up to a certain point under voluntary control, and may be varied by the will, or stopped, as when one holds one's breath.

The voluntary control of the respiratory movements is, however, limited, for if we hold our breath for any length of time, a moment soon arrives when the " necessity of respiration " overcomes the strongest will. The usual respiratory movements are carried on without our being conscious of them, and are strictly involuntary.

The rate of the respiratory movements varies according to circum-

stances, being in an adult man about 18 per minute; in most of the lower animals it is much more rapid. It varies with age, being very rapid at birth, decreasing slowly to about 30, and slightly rising towards old age. The following Table (Quetelet) illustrates this :—

A new-born infant . . .	respires	44	times	per	minute.
5 years . . .	„	26	„	„	
15—20 „ . . .	„	20	„	„	
20—25 „ . . .	„	18·7	„	„	
25—30 „ . . .	„	16·	„	„	
30—60 „ . . .	„	18·1	„	„	

Muscular exercise increases the rapidity of the respiratory movements, and, consequently, the effort of standing produces a more frequent respiration than is found in the recumbent posture. Emotions variously affect the rate and rhythm of the inspiration and expiration (*e.g.*, sighing); and, finally, morbid conditions, implicating the lungs, usually cause a greater frequency of respiration, sometimes attaining a rate of as many as 60—70 respirations per minute.

The thorax is enlarged in all directions during inspiration, the motion being usually referred to the vertical, transverse, and antero-posterior diameters respectively.

The vertical diameter is increased by the descent of the lateral portions of the diaphragm, and the slight elevation of the parts about the apex.

The lateral diameter is widened by the side-droop of the ribs being lessened; each rib is rotated upon the line uniting its extremities, and at the same time is moved upward and outward.

The antero-posterior diameter is enlarged by the general elevation of the ribs and sternum, the anterior extremities of the ribs being drawn up from their general downward incline, push the sternum forwards.

The movements of the diaphragm depress the abdominal viscera lying beneath it, and thereby distend the elastic abdominal wall and compress the gases contained in the intestines. Thus the diaphragmatic movements cause a rhythmical heaving of the abdomen. Respiration depending chiefly on the action of this one muscle is therefore spoken of as *abdominal respiration*. On the other hand, when the ribs are the chief cause of expansion of the upper parts of the chest, it is called *thoracic or costal respiration*.

These two types of respiratory movements may be imitated volun-

tarily, and are variously combined in different individuals during ordinary respiration, and in the same individual under different circumstances.

In men the general character of the ordinary quiet respiration is abdominal, the movement of the thorax being insignificant in comparison with that of the abdomen.

In women the reverse is the case; the abdominal movements are slight when compared with those of the upper part of the thorax. This difference is only well marked during quiet unconscious breathing; any forced or voluntary respiratory effort changes the typical character of man's breathing, and the costal movements become more prominent. In a forced deep inspiration the upper part of the chest shows the greatest increase in the antero-posterior diameter in both sexes.

This difference in type between male and female respiratory movements has been ascribed to different causes. The most common of these is the change brought about by the costume ordinarily adopted by females. This can hardly be an adequate explanation of the phenomenon, for we find the same type existing when the tight garments are removed, and it is apparent in those who have never been constricted by tight clothing, and even in cases where no clothing has been used, as amongst the inhabitants of hot countries; so that, though the corset may induce an exaggeration of the costal respiration, by constricting the lower ribs and interfering with the action of the diaphragm, it would not seem sufficiently to account for the normal costal type of breathing found in women.

The occasional distention of the abdomen during pregnancy has also been assigned as a cause of the female type of breathing, but it is very unlikely that pregnancy is the sole agency in producing it, since in childhood the costal type is marked in both sexes. That this type of breathing should be transmitted more markedly to females from our female ancestors is however quite possible. It is probable that the abdominal breathing of the male is also increased by hereditary transmission, but is originally due to the gradual increase in the development of the muscles of the upper extremities in males, causing a greater fixedness of the upper ribs from which they take origin.

Inspiratory Muscles.

The act of inspiration is not performed by any single muscle; indeed, even the most gentle and quiet respiration requires the co-ordinated action of many sets of muscles. Most of these muscles

have other duties to perform besides helping to produce respiratory movements.

Those which are *inspiratory* in their function are :—

1. The Diaphragm with its accessory Quadratus Lumborum to fix its origin from the last rib.
2. Levatores costarum (including the scaleni) with their accessory intercostals, which act chiefly as regulators.
3. The Serratus posticus superior.

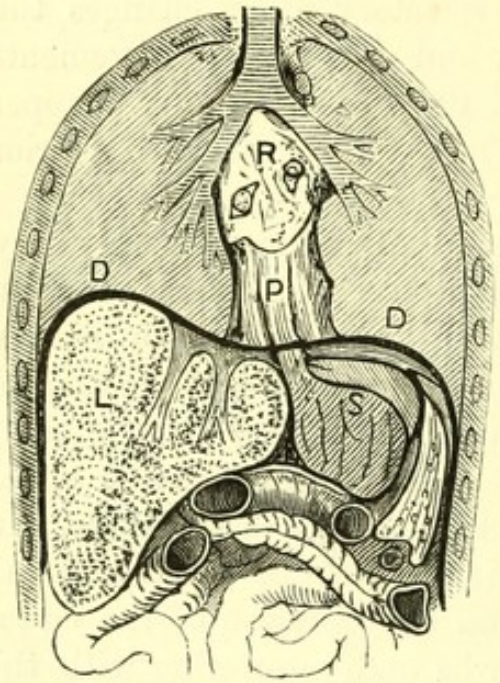


Fig. 150.—Diagram of a section made vertically from side to side through the thoracic and part of the abdominal cavities to show the position of the diaphragm, which is indicated by the dark line (D D) placed on the parts of the muscle that descend in inspiration.

P. Pericardial cavity.
L. Liver.
S. Stomach.
R. Roots of lungs cut through.

The Diaphragm is the most important inspiratory muscle. It is the only one which unaided can keep up the necessary thoracic ventilation, and, in injury of the spinal cord, owing to its isolated nervous supply, the diaphragm may be called upon to do all the inspiratory work.

During ordinary quiet breathing in the male it does the greater part of inspiration.

When not in action, one part of the muscular sheets of the diaphragm lies in direct contact with the inner surface of the lower costal part of the thoracic wall, and the other (D) is higher than the central tendon which forms the floor of the pericardium, and is fixed in one position. During inspiration these lateral parts are separated from the ribs and drawn below the level of the central tendon by the contraction of the muscular fibres. The separation is aided by the abduction of the floating ribs, which is accomplished by the quadratus lumborum and the deep dorsal muscles.

In order that the diaphragm may act to the best advantage, it is necessary that its attachments be fixed by the other muscles ; for when the quadratus lumborum, levatores and other fixing muscles are not acting, the lower floating ribs are drawn in by the diaphragm, and the power of that muscle is much diminished by the approxi-

mation of its attachments. This may be seen in spinal injuries when the inspiration is carried on by the diaphragm alone. In these cases a circular furrow marks the line of attachment of the muscle to the lower ribs and their cartilages, which are drawn inwards during each inspiration, the breathing being of course purely abdominal in type.

The *Quadratus Lumborum*, which passes from the pelvis to the last rib, has, besides the action in aid of the diaphragm just mentioned, the power of drawing down the lower outlet of the thorax, in which it is helped by other abdominal and dorsal muscles. In this action it may be regarded as the antagonist of the next group.

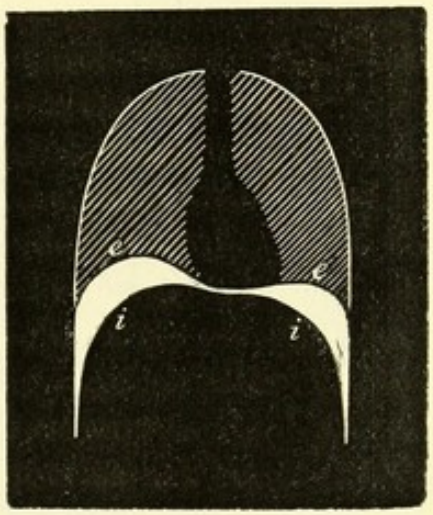


Fig. 151.—Diagram showing interval between the position of the diaphragm in expiration (*e*, *e*) and inspiration (*i*, *i*). The increase in capacity is shown by the white areas.

The *Scaleni muscles*, which pass down from the lateral aspects of the cervical vertebræ to the first two ribs, which they raise so as to draw up the upper outlet of the thorax. The quadratus and scaleni muscles thus act upon the thorax in the same way as the hands in extending a concertina.

The *Levatores Costarum* are small muscles, but on account of their number, their aggregate force is much greater than is commonly thought. They are short, thick muscles, which pass obliquely downwards and outwards from the transverse processes of the dorsal vertebræ to the angle of the ribs. Their only action is to raise the angle of the ribs, and thus diminish their anterior and lateral downward slopes ; by so doing they increase the intervals between the ribs and enlarge the lateral and the antero-posterior diameters of the chest. Thus they are purely muscles of inspiration, and probably, acting with the diaphragm and the scaleni, are the chief workers in ordinary breathing.

The *Intercostals* produce various effects on the ribs according to the different sets of muscles with which they act in association. They never act alone, and it is therefore idle to try to ascribe to them any constant specific inspiratory or expiratory action. Generally speaking, the intercostals approximate the ribs, and by this action they stiffen the thoracic wall and help to elevate the thorax when its upper part is fixed, or, when its lower part is fixed, to depress it.

Now, if both the upper and lower margins of the thorax be held firmly by strong muscles, as really occurs in inspiration—from the action of the quadratus and scaleni—the intercostals cannot approximate the ribs. Under these circumstances the results which follow their contraction will be twofold, viz. :—(1) the sternum will be pushed forwards, and the antero-posterior diameter of the thorax thus increased ; and (2) the spaces between the ribs, which are widened by the other muscles, are kept rigid and prevented from sinking inwards when the intra-thoracic pressure falls. When acting with the elevators of the ribs both intercostal layers of muscle have an inspiratory effect. But when the elevators of the ribs are passive the intercostals, acting with the anterior abdominal muscles, draw down the ribs, and act as muscles of expiration.

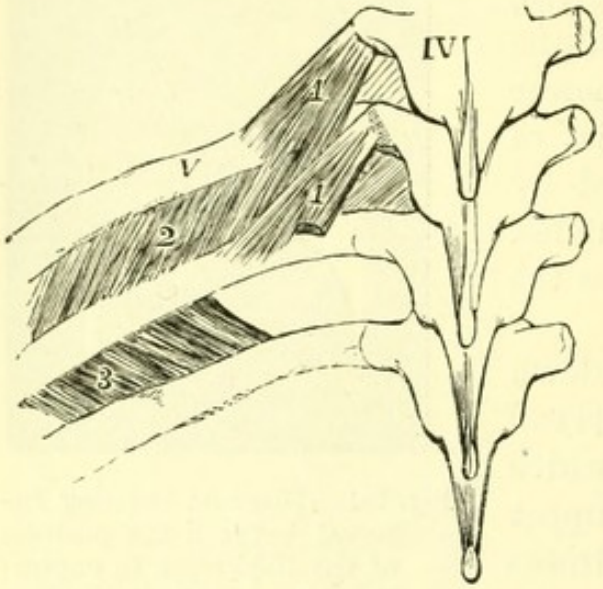


Fig. 152.—View from behind of four dorsal vertebræ and three attached ribs, showing the attachment of the elevator muscles of the ribs and the intercostals. (Allen Thomson.)

1. Long and short elevators.
2. External intercostal.
3. Internal intercostal.

Extraordinary Muscles of Inspiration. — For forced breathing a great number of muscles are called into play during the inspiratory effort, as may be seen during pathological occlusion of the air-passages, where all the thoracic, cervical, facial, abdominal muscles, and even the muscles of the extremities, are one after another, thrown into a recurring spasm before suffocation ends the patient's life.

Among the muscles which lend their aid when more energetic inspiratory movements are required, may be mentioned the *sterno-mastoid*, which helps the scaleni to elevate the front of the thoracic wall; the *pectoral* muscles and the *great serratus*, which assist when the arms are fixed.

The deep *muscles of the back*, which straighten the spine, must thereby act upon the ribs so as to elevate them and widen the intervals between them. This straightening of the dorsal curve probably helps even in quiet breathing, and no doubt has an important inspiratory influence in forced respiration. Owing to the

ribs being fixed to the sternum in front, they can only be separated laterally when the dorsal curve is lessened, and this tends to approximate the sternum and the vertebræ, thus narrowing the antero-posterior diameter of the thorax. It is in preventing this flattening of the chest that the intercostals are particularly useful; by holding the ribs together they push forwards the sternum, when the dorsal curve is extended.

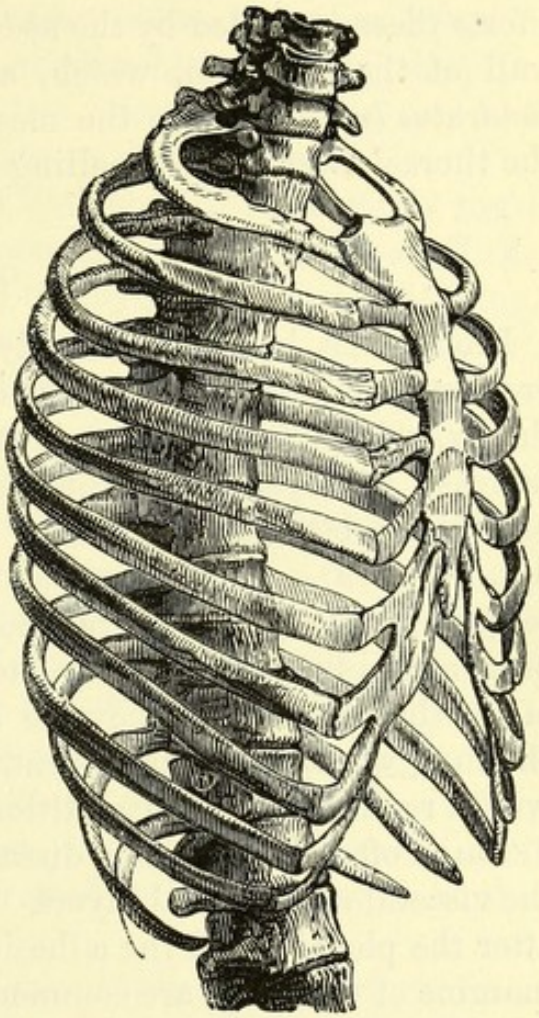


Fig. 153.—Shows the position of the Ribs and the Spinal Column in normal form of the thorax, *i.e.*, that assumed in expiration.

Expiration.

During quiet breathing *expiration* requires no muscular effort, the expulsion of the air from the chest being accomplished by the elasticity of the parts.

A powerful expiratory force is the *elasticity of the lungs*, which are on the stretch even after a forced expiration, and when distended by inspiration are capable of exerting considerable traction on the thoracic wall.

The ordinary shape of the *elastic walls* of the thorax when the muscles are not acting, corresponds with the position at the end of gentle expiration; therefore the resiliency of the muscles, costal cartilages, and other elastic tissues which are stretched during inspiration, tends to restore the ribs to the position of expiration.

The *weight of the thorax* itself, and the elastic gases in the intestinal tract, which have been compressed by the diaphragm, may also help in expiration.

After death, when the elasticity of the expiratory muscles is lost, the traction exerted by the lungs on the thorax reduces it below the size its own elastic equilibrium would tend to assume; when, therefore, air is admitted to the pleural cavity by puncture, the thorax expands slightly as the lungs shrink, and the pressure on the pleural surface becomes equal to that within the bronchi.

In forced expiration, or when the air is used during expiration for any purpose such as the production of voice, or any blowing movement, a number of muscles are called into action. The only muscles that could be called exclusively special muscles of expiration are the weak *triangularis sterni*, *serratus posticus inferior*, and parts of the intercostals; but in all violent and forcible expiratory efforts these are aided by the *abdominal muscles* forming the anterior wall of the abdomen, which, associated with the *intercostals* and *quadratus lumborum*, are the most powerful agents in drawing down the thoracic walls and expelling the air.

Function of the Pleura.

From what has been already said it is obvious that by far the greatest amount of enlargement takes place in the lower part of the thorax, while the capacity of the apex changes but little. The increase of capacity in the chest during inspiration takes place practically between the costal wall and the diaphragm (compare figs. 148, 149). If the lungs and the walls of the thorax were fused together, without the interposition of serous membranes, the different parts of the lungs would have to follow the movements of that part of the thorax to which they are attached. Thus the lower parts of the lung would be much distended during inspiration, and the apices would receive but little addition to their contained air. This condition is often found when disease of the pleura leads to adhesion of the visceral and parietal layers. When such cases live for some time after the pleurisy and the adhesions persist, the air-cells of the lower margins of the lungs are commonly found to be distended and bloodless (*i.e.*, local emphysema from habitual over-distention); while on the other hand, the apices become abnormally dense, and the alveoli are contracted and airless.

The surface of the soft elastic lung tissue is normally quite free, being encased in a serous membrane, the smooth surface of which can slide uninterruptedly and freely over the similar lining of the costal wall. That this motion of the lung actually occurs may be seen from watching the lung through the exposed parietal pleura, or recognised by studying the sounds produced by a roughness of the pleura, such as occurs in inflammation, when a "friction sound" can be detected by the ear.

The lungs move in a definite direction. From the least moveable points of the thorax, namely, the apex and vertebral margin, they pass towards the more moveable inferior costal and sternal regions.

In short, the anterior part of the lungs passes downwards and forwards to fill up the gap made by the descent of the diaphragm and by the passing of the costal wall upwards and forwards.

The position of the inferior margin of the lung may be easily recognised by percussion over the liver, and may thus be shown to move up and down with the expiration and inspiration respectively. By percussion we also find that the space between the two lungs in front is increased during expiration and diminished during inspiration, so that the heart is more or less covered by lung, and the præcordial dulness is altered every time we draw a breath.

By means of this free movement of the lungs in the cavities lined by serous membrane the air exerts equal force on the walls of all the air-cells whether they are situated in the apex or base of the lung, and the alveoli are all equally filled with air.

If the pleural cavity be brought into contact with the air, either by puncture of the thoracic walls or by rupture of the visceral pleura, the lung, owing to the great elasticity of its tissue, shrinks to very small dimensions, and the pleural cavity becomes filled with air (pneumothorax).

If air be admitted to both pleural cavities so as to produce double pneumothorax, death must ensue, for if the opening remain free the motions of the thorax only alter the quantity of air in the pleural cavity, and cannot ventilate the lungs. This demonstrates the important fact that it is the atmospheric pressure which, having access to them only through the trachea, maintains the distension of the elastic lungs, and keeps them pressed against the wall of the thorax.

The power with which the lungs can contract when the atmospheric pressure is admitted to the pleura, has been found after death, without inflation, to be six millimetres of mercury, which is probably below the pressure exerted during life, when the smooth muscle of the bronchi is acting and the tubes are free from mucus, for this rapidly collects in the minute air-tubes at death, and impedes the outflow of air.

When the lungs are inflated before the pleura is opened, the pressure can easily be made to rise to nearly $1\frac{1}{4}$ inches (30 mm. mercury).

From this it would appear probable that when the lungs are stretched by inspiration they exert a negative pressure equal to 30 mm., and when the lungs are in a position of expiration they still tend to contract with a force of 6 mm. mercury.

Pressure-Differences in the Air.

The immediate effect of the increase in capacity of the chest is that a pressure-difference is established between the interior of the thoracic cavity and the atmosphere.

The reduction in pressure produced in the lungs and air-passages by inspiratory movements, or the increase of pressure accompanying expiration, is very slight during ordinary quiet breathing with free air passages. But the least impediment to the entrance or to the exit of the air at once makes the difference very notable.

It is difficult to obtain an accurate experimental estimate of the variations in the pressure in different parts of the air-passages during quiet breathing, because even the most careful attempt to measure the pressure causes an increase which is still further magnified by the sensitive muscular mechanism of the air-passages.

The variations in pressure occurring in the pulmonary air are greatest in the alveoli, and gradually diminish towards the larger air-tubes, so that they disappear at the nasal orifice, where, if no impediment be placed to the course of the air, the pressure will remain very nearly equal to that of the atmosphere. By connecting one nostril with a manometer and breathing through the nose with the mouth shut, it can be shown that inspiration causes a negative pressure of about 1 mm. mercury, and expiration a positive pressure of 2 to 3 mm. ; these results must be divided by two, since by plugging one nostril they shut off half the normal inlet. Forced inspiration and expiration give respectively — 57 and + 87 mm.

This great difference depends on the elastic forces against which the inspiratory muscles act in distending the thorax, all of which assist in expiration.

The Volume of Air.

During ordinary respiration the volume of the inspiratory and expiratory stream of air is surprisingly small when compared with the volume of air sojourning in the lungs.

After an ordinary expiratory act we can force out a great quantity of air by a voluntary effort ; but even after this is got rid of the lungs are still well filled. Some of this *residual* air, which never leaves the chest during the life of the animal, is pressed out by the elasticity of the lungs when the pleura is opened. But a certain amount of air cannot be removed in any way from the alveoli. Even

when the lung is cut out of the chest and divided into pieces, enough air is retained in the air-cells to render it buoyant. This fact is relied on by medical jurists as an evidence that an infant has been born alive and distended the lungs with air, for except breathing has been well established, the tolerably fresh lung of an infant will sink in water.

In order to have a clear idea of the volumes of air at rest and in motion during pulmonary ventilation it is convenient to follow the classification from which the nomenclature in common use has been borrowed.

Tidal air is the current of air which passes in and out of the air-passages in quiet natural breathing. It amounts to about 500 cc. (30 cubic inches).

Reserve air is that volume which can be voluntarily emitted after the end of a normal *tidal* expiration, and which, therefore, during ordinary respiration remains in the lungs ; it is estimated at about 1500 cc. (or nearly 100 cubic inches).

Complemental air is that which can be voluntarily taken in after an ordinary inspiration by a forced inspiration ; it also amounts to about 1500 cc., but is not used during ordinary breathing.

Residual air is the volume which remains in the lungs after a forced expiration, that is to say, which no voluntary effort can remove from the lungs ; it includes the air which leaves the lungs when the pleura is opened after death and the air which persistently remains in them after they have collapsed. This amounts to about 2000 cc. (or about 120 cubic inches).

Vital capacity is a term meaning the greatest amount of air that can be emitted by a forced expiration immediately following a forced inspiration, so that it equals the sum of the tidal, reserve, and complemental air. The vital capacity is estimated by spirometers of different kinds, and gives an approximate measurement of (1.) The capacity of the chest. (2.) The power of the respiratory muscles. (3.) The resistance offered by the elasticity or rigidity of the walls of the thorax. (4.) The working capacity of the lungs, *i.e.*, their extensibility or freedom from disease. It, therefore, varies greatly according to the age, sex, position of the body, the occupation, weight, height, the fulness of the hollow viscera of the abdomen, and the pathological condition of the lungs. It can be much increased by practice, and this fact, apart from the injury forced respirations may produce in a morbid state of the lung, renders it inapplicable as a gauge of pulmonary disease.

Diffusion.

From the foregoing it appears that the volume of air habitually sojourning in the lungs during natural respiration, or *stationary air*, is about 3,500 cc. (nearly 220 cubic inches), while the fresh air introduced by each inspiration is only a little over 500 cc. (30 cubic inches), or, in other words, about one-seventh of the air in the lungs is changed at each breath. Indeed, the 500 cc. of air is only just sufficient to fill the trachea and larger bronchial passages, so that the fresh air does not reach the pulmonary alveoli, or directly replace any of the air they contain. The tidal stream is, however, brought into immediate relation with the stationary air, and the thoracic movements cause them to mix mechanically, so that rapid *diffusion* takes place in the minute bronchi. Diffusion is also constantly occurring between the air of the small tubes and the terminal sacs, and it alone suffices to maintain the necessary standard of purity in the air of the alveoli. If the harmless gas, hydrogen, be inhaled during *one* inspiration, it requires 6 to 10 respirations to get rid of the impurity from the expired air. From this it has been inferred that this number of respiratory acts would be necessary to render the air in the alveoli quite pure even if no fresh impurities were allowed to enter from the blood.

Respiratory Sounds.

As the streams of air enter the air-passages and lungs they produce sounds which are of the greatest importance to the physician, owing to the manner in which they become altered by disease.

A sound called "bronchial breathing" is produced in the large bronchi and trachea, and is like the noise of air blowing through a tube. This can normally be heard over the trachea, or at the back between the shoulder-blades over the entrance of the large bronchi into the root of the lung.

Another sound called "vesicular" can be heard all over the chest, being most distinct where the lung is most superficial, and where other sounds are absent, as in the sub-axillary region. It is a gentle rustling sound caused by the air passing into the infundibuli. It varies much with the force of respiration and many other circumstances. In children up to ten or twelve years of age it is remarkably sharp and loud, and is called "puerile breathing."

Nervous Mechanism of Respiration.

The movements of respiration go on rhythmically without any voluntary effort, and even when we are quite awake they occur

almost without our being conscious of them, and repeated variations take place in the rate, depth, and general type of our respirations without our knowledge. Indeed, if this self-regulating arrangement did not exist we should have to devote our attention to adapting our respiratory movements to the ever-varying requirements of the gas-interchange of the blood.

Like all other groups of skeletal muscles, those which act on the thorax are regulated by nerves, and work together in harmony. The co-ordinated movements are so far under the control of the will that any of the groups of muscles may be employed separately, or in conjunction.

But the respiratory differ from the other skeletal muscles, in that they undergo rhythmical co-ordinated contractions which are not directed by our will, and can be influenced only to a certain extent by it, for they cannot be made to cease altogether.

Respiratory Centres.

The normal, rhythmical, co-ordinated movements of respiration are not only brought about, but are also regulated by an involuntary nervous mechanism. Since we are unconscious of its action, it certainly is not dependent on the voluntary centres. The upper parts of the brain cannot be needed for regular breathing, since (1) animals born with deficiently developed brains breathe rhythmically; and (2) removal of the brain of birds, &c., or loss of voluntary movement in man (hemiplegia), causes no interruption of the respiratory movements. Injury to the upper part of the spinal cord causes death by stopping respiration. The regulating *centre* must then be lower than the cerebral centres, and higher than the cervical part of the spinal marrow. The direct evidence of the seat of this centre was found by Flourens, who showed that a localised spot exists in the medulla oblongata, injury of which causes instant cessation of the respiratory movement.

This vital point, *nœud vital*, is situated in the floor of the fourth ventricle, near the point of the *calamus scriptorius*, and is now commonly spoken of as the respiratory centre. It is convenient to suppose that there are two groups of cells, one presiding over the inspiratory, and the other over the expiratory, muscles.

From this centre the impulses which give rise to the all-important respiratory movements rhythmically pass down the spinal cord and nerves. So long as the nervous communication between the centre and the muscles is intact the movements go on with undisturbed

regularity; if it be cut off, or the centre be destroyed, respiration instantly stops.

Excitation of Respiratory Centre.—What keeps this centre active? It has been already stated that all the conditions of the body which cause an increased tissue change, use up a greater amount of oxygen and give off more carbonic acid, therefore are accompanied by more active movements of the respiratory muscles. From this it would appear that there exists some relation between the activity of the respiratory centre and the condition of the blood, a deficiency of oxygen or an excess of carbonic acid gas calling forth increased action. One has only to hold one's breath as long as possible, and note the series of rapid and deep respirations that follow such a temporary impediment to the proper oxygenation of the blood, in order to see that this involuntary respiratory centre is profoundly influenced by a deficiency of oxygen. Experimentally it can be shown that the centre is excited, in a great measure, at least, by the poorly oxygenated blood flowing through the medulla, and possibly also by the action of the venous blood circulating through distant organs, and reflexly affecting the centre. It has also been shown that the temperature of the blood circulating through the medulla affects the activity of the centre, for, if the blood in the carotids be warmed, the respiratory movements become more rapid.

The respiratory centre is a good example of what is called an "automatic nerve centre," not depending upon the arrival of nerve impulses from afar for its excitation, nor merely reflecting the influences of other centres, but acquiring its energy from its nutritive income and the thermal condition of the warm blood which flows through it.

So long as the amount of oxygen flowing through the centre is kept up to a certain standard, the normal excitability of the centre continues, and we have natural quiet breathing, called *Eupnœa.* When the oxygen falls below the normal standard, the respiratory centre becomes more excitable, and more active movements or "difficulty of breathing" called *Dyspnœa* is produced.

If the theory that a deficiency of oxygen is the normal stimulus to action of the respiratory centre, be correct, a superabundant quantity should diminish the activity of the centre, and a condition the opposite of dyspnœa would be produced. This is difficult to show in natural breathing, though every one knows the efficiency of taking a few deep breaths before a dive into water or an attempt to hold the breath. With artificial breathing, if the movements be carried on very energetically for some time, and then be stopped, the

animal will not at first attempt to breathe, but after a short time, somewhat less than a minute, gentle and slow respiratory movements commence. This cessation of breathing, called *apnœa*, depends upon the blood being so charged with oxygen that it no longer acts as a stimulus to the centre.

It is probable that dyspnœa is produced by a deficiency in oxygen rather than by an excess of carbonic acid gas. This is proved by the fact that it occurs when the carbon dioxide is removed from the blood by breathing air which is free from CO_2, and is only deficient in oxygen, and, secondly, because an excess of CO_2 gas in the air causes a drowsy condition rather than an active dyspnœa.

Regulation of Respiratory Activity.—Although the respiratory centre is in the common sense *automatic*, yet it is constantly affected by many influences coming from other parts, which reflexly modify the respiratory movements. Thus mental *emotions* variously influence both the rate and depth of breathing, sometimes causing more rapid and sometimes slower respiratory action. The application of stimulus to almost any part of the *air-passages* completely changes the respiratory rhythm, as may be seen by irritating the nasal mucous membrane. The ordinary *sensory nerves* passing from the *skin* are also capable of exciting respiratory movements. This is well shown by the gasping that follows the sudden application of cold to the body. It is along these sensory nerves that one tries to transmit impulses by applying mechanical, thermal, or other stimulus to the skin of a new-born infant, whose respiratory centre having been kept long in the condition of apnœa, is slow to respond to an exciting influence caused by a deficiency of oxygen.

Experiment proves that most, if not all, afferent nerves can affect the respiratory centre, either by increasing or reducing its activity; but there is one special nerve, namely, the *pneumogastric* or *vagus* and its branches, which have both these capabilities developed to such a degree that they must be regarded as the regulating nerves of respiration.

Though section of *one* vagus has little or no effect on respiration, if the *two* vagi be cut a marked change takes place in the respiratory rhythm. The rate of the inspiration is reduced to less than half the normal rate, while each breath becomes deep and prolonged, so that the respiratory function of the lungs goes on for some time unimpaired, and the hæmoglobin of the blood receives the due amount of oxygen. Although the character of the breathing is completely changed, from the rapid gentle motion of natural respiration to a series of slow deep gasps, the air volumes per minute and the

chemical changes remain the same. If the central end of the cut vagus be now stimulated gently, the rate of the respiratory move-

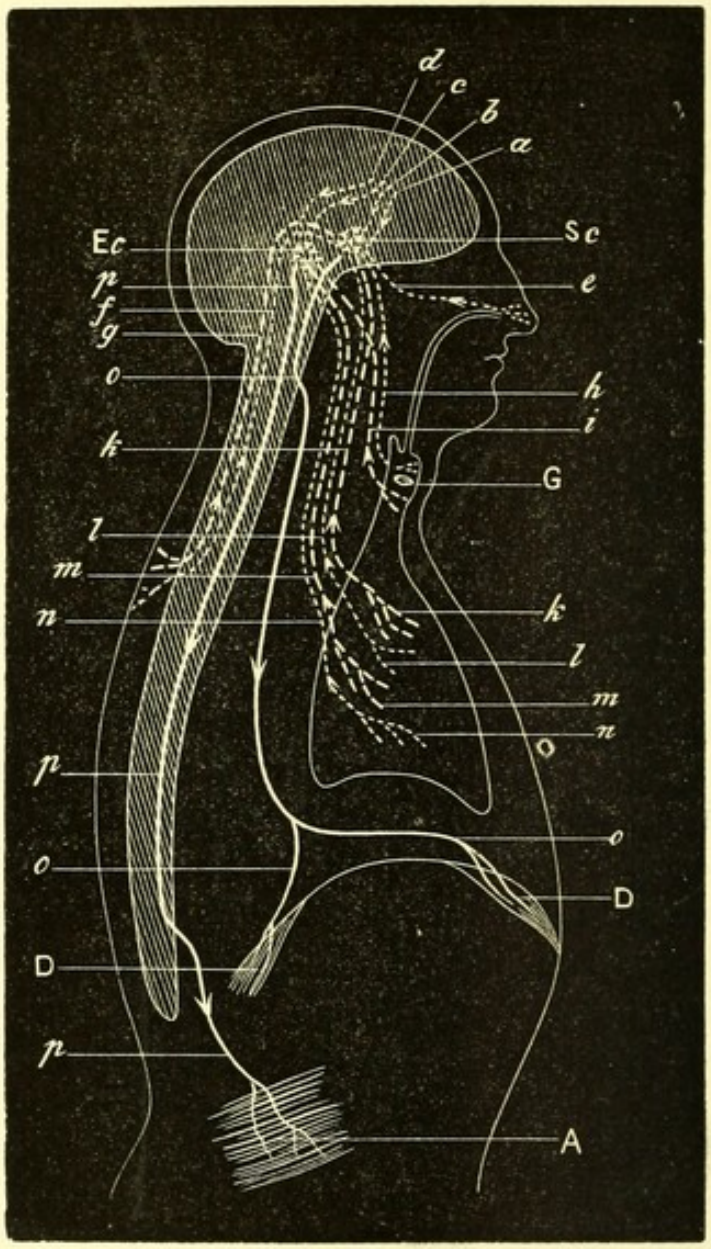


Fig. 154.—Diagram of the Nervous Mechanisms of Respiration. (After Fick.)

Sc. Centre for inspiratory movements, from which pass efferent channels, represented by the continuous white line (*o*) to the inspiratory muscles represented by the diaphragm (D).

Ec. Centre for expiratory movements, from which efferent channels (*p*) pass down the cord to the muscles of expiration, represented by the abdominal muscles (A).

To both these centres *afferent* impulses of two kinds come from the cerebral centres (*a*, *b*, *c*, *d*) to check or excite activity. These voluntary impulses may be called afferent as far as the respiratory centres are concerned. From the cutaneous surface (*f*, *g*) and the nose (*e*), impulses arrive, which modify the action of the inspiratory centre. From the larynx (G) come checking impulses (*h*) to the inspiratory, and exciting impulses (*i*) to the expiratory centre. And, finally from the lungs come both exciting and inhibiting impulses (*k*, *l*, *m*, *n*) to both the expiratory and inspiratory centres, and by these channels the rhythm of ordinary breathing is regulated.

ments may again be quickened to the normal. If the stimulus be very strong, respiratory spasm can be produced. On the other hand, if the central end of the cut superior laryngeal branch of the vagus be stimulated, breathing becomes slow, and can be made to cease in the position of ordinary expiration, while a violent spasm of the laryngeal and expiratory muscles is caused.

So that in the pneumogastric nerve, fibres exist which convey impulses of two kinds to the inspiratory centre; the one increases its excitability and hastens the discharges of inspiratory impulses, the other decreases its irritability and checks the inspiratory movement. The marked change just described as occurring when the two pneumogastrics are cut proves that these afferent influences are *constantly* at work, quickening the respiratory rhythm. We may assume that the slow, deep respirations which follow section of the vagi are caused by the un-regulated automatic action of the inspiratory centre. No impulse is discharged until the venosity of the blood in the centre arrives at a certain point, and then the accumulated energy is sent to the respiratory muscles, and a deep gasping inspiration occurs, and thus each respiratory act is called forth by the blood becoming so venous as to act as a powerful stimulus.

So long as the centre is stimulated by the regulating influence of the vagi this venous condition is not allowed to occur, the intense excitation of the centre is thereby prevented, and the necessary movements performed with a minimum of muscle energy.

The exact mode of stimulation of the pulmonary terminals of the afferent fibres of the pneumogastric is not certain. It has been suggested that distention or retraction of the lungs may act as a mechanical stimulus to fibres inhibiting and exciting respectively the inspiratory centre. Each expansion of the lungs calls forth the ensuing relaxation, and the relaxed state, in its turn, induces a new inspiration, and thus the lungs themselves are able to guide the thoracic movements by means of the pneumogastrics.

The expiratory part of the centre probably takes no part in ordinary breathing, but is called into play in dyspnœa, vocal use of the expiratory blast of air, and in various modified respiratory movements.

Modified Movements of the Respiratory Muscles.

Besides the ordinary respiratory motions and the voluntary modifications made use of in speaking, singing, &c., the muscles of

respiration perform a series of movements of an involuntary reflex nature indicative of certain emotions and mental states.

They will be seen to resemble each other in the mechanism of their production, though differing essentially in expression. The following are the more important :—

Coughing is caused by a stimulus applied to certain parts of the air-passages, but more particularly to the larynx ; the stimulus passing along the superior laryngeal branch of the pneumogastric. It consists of a deep inspiration, closure of the glottis, and then a more or less violent expiratory effort, accompanied by two, three, or more sudden openings and closures of the glottis, so that rapidly repeated blasts of air pass through the upper air-passages and mouth, which is generally held open.

Sneezing is caused by a stimulus applied to the nose or eyes, the impulses being carried to the respiratory centre by the nasal and other branches of the 5th nerve. It consists of a deep inspiration and closure of the glottis, followed by a single explosive expiration and sudden opening of the glottis and posterior nares and facial distortion.

Sneezing is a purely reflex act, since it is impossible to produce it voluntarily, except indirectly by the stimulation of the nasal mucous membrane with some irritating substance.

Laughing consists of a full inspiration, followed by a long series of very short rapid expiratory efforts. The facial muscles are at the same time thrown into a characteristic set of movements.

Crying is made up of a series of short sudden expirations, accompanied by peculiar facial contortions, lachrymal secretion, and usually associated with the following.

Sobbing consists of a rapid series of convulsive inspiratory efforts, causing but little air to enter the chest, followed by one long expiration.

Sighing is a long slow inspiration, quickly followed by a corresponding expiration.

Yawning is a very long deep inspiration, completely filling the chest. It is accompanied by a peculiar depression of the lower jaw, wide open mouth, facial movements, and commonly stretching of the limbs.

Hiccough is an unexpected inspiratory spasm, chiefly of the diaphragm, the entrance of the air being checked by the sudden closure of the glottis.

CHAPTER XIX.

THE CHEMISTRY OF RESPIRATION.

THE simplest way to investigate the study of the gas interchange that takes place in the lungs, between the air and the blood, is to compare the composition of the expired air with that of the atmosphere, and from the alteration found to have taken place during the tidal current we arrive at the changes which the air undergoes during its journey in and out of the air-passages, and we then examine the venous and arterial blood in order to ascertain the changes the blood undergoes in becoming arterial.

The atmosphere is made up of a mixture of nitrogen and oxygen with a variable amount of moisture and a minute proportion of carbonic acid.

The following table gives the *volume** of the gases in dried air :—

Oxygen . . .	20·96 per cent.,	or about	21 per cent.
Nitrogen . . .	79·02 „	„	79 „
Carbonic dioxide	0·02—0·06 „	„	4 parts in 10,000.

The amount of moisture contained in the air is very variable, and depends in a great measure upon the temperature and the direction of the wind. The dampness of the air depends upon the temperature, so that air containing the same absolute amount of moisture may be relatively dry or damp, according as the temperature rises or falls. As a general rule the air is relatively dry, that is to say, it does not contain so much moisture as it is capable of taking up in the form of aqueous vapour at its ordinary temperature. At certain times of the day the air may be saturated owing to a sudden fall of temperature.

The temperature of the air which we breathe varies considerably,

* On account of the difference in the atomic weights, the atmosphere being only a *mechanical mixture* of the gases, the proportion by *weight* is slightly different, being about—Oxygen 23 per cent., Nitrogen 77 per cent.

according to the season of the year, &c., but almost always in this country it is lower than that of our bodies.

Expired Air.

The following are the notable characters in the tidal air on its leaving the air-passages :—

1. It is rich in CO_2, containing in quiet breathing on an average 4·38 per cent. instead of ·04 per cent.

2. It is poor in O, containing about 4·5 per cent. less than the atmosphere, *i.e.*, 16·46 per cent.

3. A slight increase in the N. has been observed, possibly the outcome of nitrogenous metabolism.

4. The temperature of the air is approximated to that of the body, and it therefore commonly exceeds the temperature of the air inspired. The air on leaving the air-passages is about 36·5° C. This is not much influenced by the temperature of the atmosphere, as may be seen from Valentine's Table :—

Temperature of the Atmosphere and of Expired Air.

−6·3° C.	=	+29·8° C.
+17·0° C.	=	+36·2° C.
+44·0° C.	=	+38·5° C.

It can be seen from the last statement that very hot air (+44° C.) if breathed is cooled in its transit through the air-passages.

5. In quiet breathing the expired air is saturated with moisture ; in rapid breathing this is not the case. It must be remembered that the air when warm is capable of holding a greater quantity of vapour than when it was inspired. The difference can be best appreciated in cold weather, when the vapour of the warm expired air is condensed on meeting the cold atmosphere. Great quantities of water and heat are given off in producing this saturation.

6. If the tidal air be dried and cooled and measured at a certain pressure before and after respiration, it is found that the expired air has lost about $\frac{1}{50}$ of its volume. But owing to the expansion from the increased temperature and the presence of the vapour, the volume of air when expired is greater than that inspired.

If the oxygen were all used to make CO_2, these volumes ought to be the same, for the volume of CO_2 is equal to that of the O it contains, if set free. The volume CO_2 given off is, however, only about 4·38, to 4·5 volumes of O taken in, so that part of the O must be used in some other way, probably in forming H_2O and urea.

7. The expired air is also said to contain traces of the following impurities :—(1) ammonia, (2) hydrogen, (3) carburetted hydrogen (CH_4), (4) organic matter. These, and probably other impurities, give the breath its peculiar odour and noxious properties, for an atmosphere rendered "stuffy" by expired air is much more injurious to health than an atmosphere in which a similar deficiency of O or excess of CO_2 had been artificially produced by chemical means; this fact ought to be remembered when calculating the ventilation required for hygienic purposes. The following Table may assist in comparing the atmosphere with the expired air :—

	Atmosphere.	Expired Air.	Difference.
CO_2	·04 per cent.	4·38 per cent.	+ 4·34
O	20·81 ,,	16·03 ,,	− 4·78
N	79·15 ,,	79·55 ,,	+ ·40
Temperature	−6° *C.*− + 25° *C.*	29·8° *C.*−38·5° *C.*	
Moisture	about 10 grms. to 1 cubic metre.	about 40 grms. to 1 cubic metre.	
Volume	.....	Apparently increased, absolutely reduced $\frac{1}{50}$th.	
Impurities	.....	NH_3, H, CH_4, and poisonous organic matter.	

About $\frac{1}{7}$th of the O which is used does not take part in the production of the CO_2, but this proportion may vary greatly. Thus the estimation of the CO_2 can give no sure guide to the amount of O taken up ; and each gas has to be estimated separately if an accurate measurement be required.

The average amount per diem may be said to be :—

Carbon dioxide given off about	. . .	800 grammes.
Oxygen consumed	,, . . .	700 ,,
Water given off	,, . . .	500 ,,

The amounts of O taken up and of CO_2 given off, differ in different individuals and in the same individuals under varying circumstances, among which the following may be enumerated :—

1. Increase in the rapidity or the depth of respiratory movements, accompanied by an increase in the tidal stream, produces an increase of the total amount of CO_2 given off, while the percentage in the volume of expired air is diminished.

2. It varies with age. The amount increases with age up to 30 years, and then remains constant.

3. Sex ; is less in women than in men, but it increases in pregnancy.

4. With muscular activity it is notably increased.

5. Change of temperature of the air has a marked influence on the CO_2 output of cold-blooded animals, which is increased in direct proportion to the elevation of temperature. The effect on warm-blooded animals is the opposite, so long as they can regulate their temperature. The sustentation of the body temperature in cold weather is accompanied by a distinct increase in the output of carbon dioxide.

6. The time of day; a maximum is arrived at about midday and a minimum about midnight.

7. An increase in the amount of carbon dioxide in the atmosphere diminishes the amount given off from the lungs.

Changes the Blood undergoes in the Lungs.

In order to understand how the oxygen and the carbonic acid pass to and from the blood in the pulmonary capillaries we must know the relationship of these gases to the blood in the arterial and venous sides of the circulation.

In the chapter on the blood (pp. 157, 158) it is stated that both the oxygen and the carbon dioxide can be removed from the blood by the mercurial air-pump, and that the greater part of these gases are chemically united with some of the constituents of the blood, and that a different quantity of each gas is found in arterial and venous blood. Now that we know the change from the venous to the arterial condition to take place during the passage of the blood through the pulmonary capillaries where it is exposed to the air, we may assume that the acquisition of oxygen and the loss of CO_2 form the essential difference between venous and arterial blood.

From either kind of blood about 60 volumes of gas may be extracted from every 100 volumes of blood with the mercurial gas-pump. The composition of this gas varies considerably in venous, but not very much in arterial blood. An average is given in the following Table :—

	O vols. %.	CO vols. %.	N vols. %.
Arterial . .	20	39	1—2
Venous (about) .	8—10	46—50	1—2

The more rapidly after bleeding the gases are removed the greater is the proportion of O that can be obtained; as delay allows some of it to combine with easily oxidised substances in the blood itself. The amount of oxygen varies in different parts of the venous system.

In the blood of an animal dying of slow asphyxia only traces of oxygen can be found and these soon disappear after death.

The proofs that O is, for the most part, in chemical combination with the hæmoglobin of the red blood corpuscles, and not merely absorbed, as one might be led to suppose from its coming away when the pressure is reduced, are numerous and satisfactory.

1. When arterial blood is submitted to gradual diminution of pressure in the mercurial air-pump the oxygen does not come away in accordance with the established law of the absorption of gases (Henry–Dalton) by coming off in proportion to the diminution of the pressure. At first only traces appear (probably the small amount really dissolved), and when the pressure has been reduced to a certain point, about $\frac{1}{5}$th of that of the atmosphere, the oxygen comes off suddenly; after which little more can be obtained by further reduction of pressure. Hæmoglobin combines with O in the same way, very rapidly at first even when the pressure is low.

2. If the oxygen were only in a state of absorption, the blood while passing through the pulmonary capillaries, could only take up about 0·4 volume per cent., which would be inadequate for life. We know that the quantity of O going to the blood from the air in the alveoli cannot well be explained on physical grounds alone; and, when an animal dies of asphyxia from want of ventilation in a limited space, all the O of the air in the space is absorbed. Since the partial pressure of the O in the chamber falls to zero while some still exists in the hæmoglobin, it cannot be the pressure which makes the O pass into the blood.

3. Another conclusive proof that the union of the O with the hæmoglobin is really a chemical one, is given by the spectroscopic examination of a hæmoglobin solution. When deprived of its O, and after the admixture of the air, quite dissimilar spectra are seen, as already pointed out in Chapter XIV. (Fig. 155, p. 298.)

4. The amount of O taken up by the blood is not always in proportion to the pressure of that gas, but rather to the amount of hæmoglobin in the blood; and we therefore find the adequacy of the respiratory function of the blood going hand in hand with its richness in hæmoglobin, and thus the "shortness of breath" of anæmic and chlorotic individuals is explained.

5. The oxygen can be displaced by the chemical union of other gases with the hæmoglobin.

Our knowledge concerning the relation of the CO_2 to the constituents of the blood is less definite.

It does not all exist as a mere physical solution, for it comes

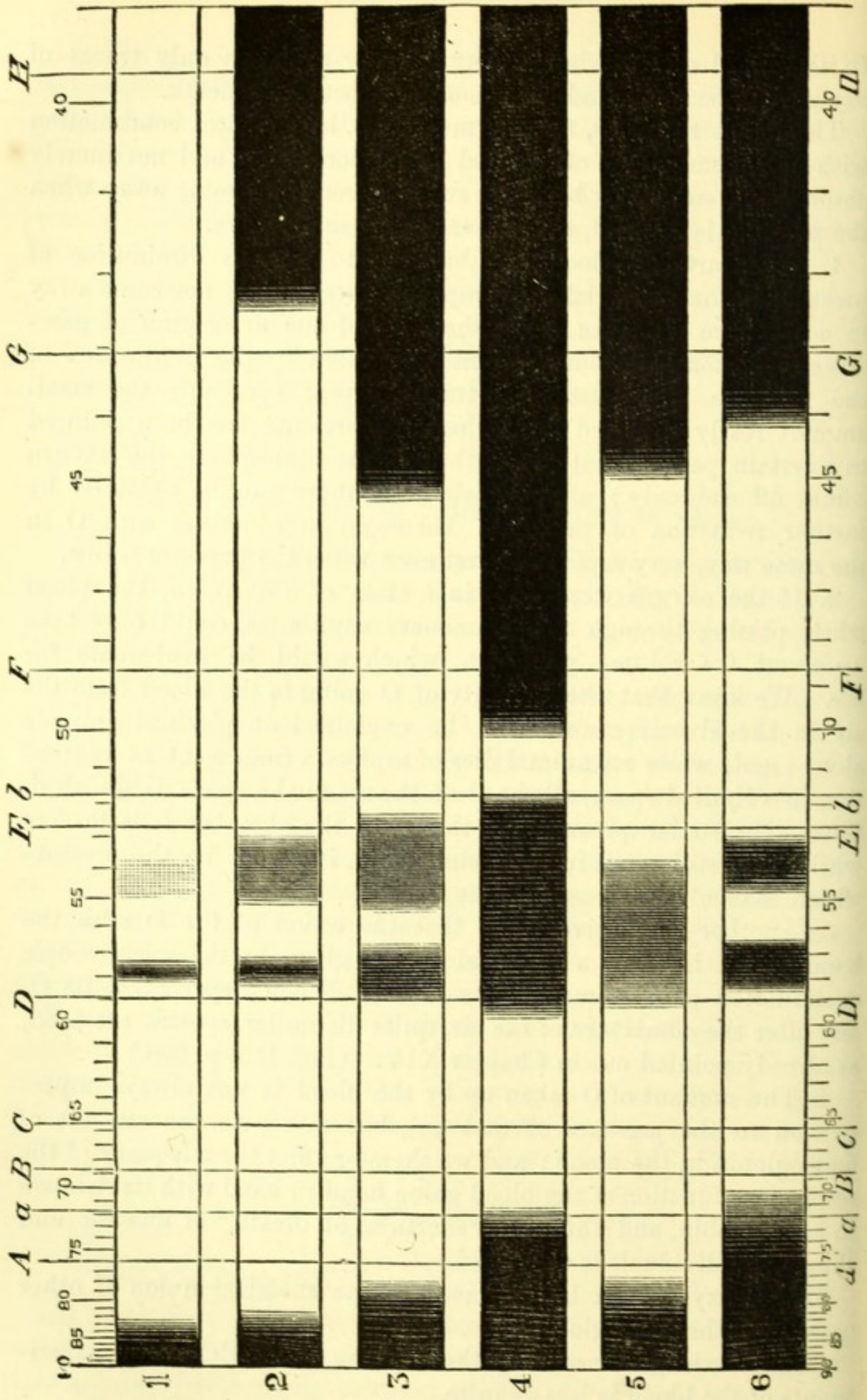


Fig. 155.—Spectra of Oxyhæmoglobin, reduced hæmoglobin, and CO-hæmoglobin. (Gamgee.)
1, 2, 3, and 4. Oxyhæmoglobin increasing in strength or thickness of solution.
5. Reduced hæmoglobin. 6. CO-hæmoglobin.

off irregularly under the air-pump, and does not exactly obey the Henry-Dalton law of the absorption of gases. Part comes off easily and part with difficulty. It is not associated with the corpuscles, for more of this gas can be obtained from serum than from a like quantity of blood. It is more easily removed from the blood than from the serum, a certain proportion (about 7 per cent. of the whole) remaining, in the serum in vacuo, until dissociated by the addition of an acid or a piece of clot containing corpuscles. If bicarbonate of soda be added to blood from which all the gas has been removed, still more CO_2 can be pumped out, from which it would appear that something exists in the blood capable of dissociating CO_2 from sodium bicarbonate.

It has been suggested that the CO_2 is in some way associated (possibly as sodium bicarbonate) with the plasma of the blood, and that the corpuscles have the power of acting like a weak acid, and of dissociating it from the soda, and thus raising its tension in the blood.

The great importance of the chemical nature of the union between the O and hæmoglobin for external respiration becomes most striking when the actual manner in which the entrance of the O is effected is taken into account.

It must be remembered that the further we trace the air down the passages, the less will be the percentage of O found in it, and, therefore, a less pressure exerted by that gas. This is shown by the fact that the air given out by the latter half of a single expiration has less O and more CO_2 than that of the first half. The most impure air lies in the alveoli of the lungs, for, since the tidal air scarcely fills the larger tubes, the air in the alveoli is only changed by diffusion with the impure air of the small bronchi. Any impediment to the ordinary ventilation of the alveoli so reduces the percentage, and, therefore, the tension of the O, that it would probably sink below that in the blood, and in that case, were it not a chemical union, the O would escape more readily from the blood in proportion as its tension in the blood exceeded that of the air of the alveoli. We know, however, that the blood retains a considerable quantity of oxygen even in the intense dyspnœa of suffocation.

In the same way the difference of tension of the CO_2 in the alveolar air and in the blood, hardly explains the steady manner in which the CO_2 escapes, and it has, therefore, been suggested that this escape also depends in some way upon a chemical process, possibly connected with the union of the O and hæmoglobin; because the admission of O to the blood seems to facilitate the exit of the CO_2.

The following table gives the approximate tension of the two gases in the different steps of the interchange in the case of dogs with a bronchial region occluded so that the air it contained could be examined. It shows that the tensions are such as to enable physical absorption to take some share in the entrance of the O as well as in the escape of the CO_2. A separate column gives the volumes per cent. of each gas, corresponding to these tensions as compared with the atmospheric standard. The physical process must occur before the oxygen and the hæmoglobin meet, since the latter is bathed in the plasma, and further separated from the alveolar O by the vessel wall and epithelium.

	CO_2		O	
	Tension in mm. Hg.	Corresponding Volume per cent.	Tension in mm. Hg.	Corresponding volume per cent.
In arterial blood....	21·	2·8	29·6	3·9
In venous blood	41·	5·4	22·	2·9
In air of alveoli	27·	3·56	27·44	3·6
In expired air.. ...	21·	2·8	126·2	16·6
In atmosphere	0·38	0·04	158·	20·8

Internal Respiration.

The arterial blood, while flowing through the capillaries of the systemic circulation and supplying the tissues with nutriment, undergoes changes which are called internal or tissue respiration, and which may be shortly defined to be the converse of pulmonary or external respiration. In the external respiration the blood is changed from venous to arterial; whereas in internal respiration the blood is again rendered venous.

There can now be no doubt that these chemical changes take place in the tissues themselves, and not in the blood as it flows through the vessels. The amount of oxidation that takes place in the blood itself is indeed very small. The tissues, however, along with the substances for their nutrition, extract a certain part of the O from the blood. In the chemical changes which take place in the tissues, they use up the oxygen, which rapidly disappears, the tension of that gas becoming very low; at the same time other chemical changes are indicated by the appearance of CO_2. The disappearance of the O and the manufacture of CO_2 do not exactly correspond in amount, and they doubtless often vary in different parts and under different circumstances. Of the intermediate steps in the tissue

chemistry we are ignorant. We do not know the way in which the oxygen is induced by the tissues to leave the hæmoglobin ; we can only say that the tissues have a greater affinity for O than the hæmoglobin has, and they at once convert the O into more stable compounds than oxyhæmoglobin, and ultimately manufacture CO_2, which exists in the tissues and fluids of the body at a higher tension than even in the venous blood.

Respiration of Abnormal Air, &c.

The oxygen income and carbonic acid output are the essential changes brought about by respiration, therefore the presence of oxygen in a certain proportion is absolutely necessary for life. The 21 per cent. of O of the atmosphere suffices to saturate the hæmoglobin of the blood, and 14 per cent. of O has been found to be capable of sustaining life without producing any marked change in respiration.

Dyspnœa is produced by an atmosphere containing only 7·5 per cent. of O. This dyspnœa rapidly increases as the percentage of O is further decreased, and when it gets as low as 3 per cent. suffocation speedily ensues.

The output of CO_2 can be accomplished if the lungs be ventilated by any harmless or indifferent gas, and since the manufacture of the CO_2 does not take place in the lungs, its elimination can go on independently of the quantity of O in them. The 79 per cent. of N contained in the atmosphere has a passive duty to perform in diluting the O and facilitating the escape of the CO_2 from the lungs.

Indifferent gases are those which produce no unpleasant effect of themselves, but which, in the absence of O, are incapable of sustaining life, such as nitrogen, hydrogen, and CH_4.

Irrespirable gases are such as, owing to the irritating effect on the air passages, cannot be respired in quantity, as they cause instant closure of the glottis. In small quantities they irritate and produce cough, and if persisted in, inflammation of the air passages ; among these are chlorine, ammonia, ozone, nitrous, sulphurous, hydrochloric, and hydrofluoric acids.

Poisonous gases are those which can be breathed without much inconvenience, but when brought into union with the blood cause death. Of these there are many varieties. (1.) Those which permanently usurp the place of oxygen with the hæmoglobin, viz. :— carbon monoxide (CO), hydrocyanic acid (HCN). (1.) Narcotic : (*a*) carbonic dioxide (CO_2), of which 10 per cent. is rapidly fatal, 1·0

per cent. is poisonous, and over 0·1 per cent. injurious. (β) nitrogen monoxide (N_2O). Both of these gases leads to a peculiar asphyxia without convulsions. (γ) chloroform, ether, &c.

(3.) Sulphuretted hydrogen (H_2S), which reduces the oxyhæmoglobin, and produces sulphur and water.

(4.) Phosphuretted hydrogen (PH_3), arseniuretted hydrogen ($As H_3$), and cyanogen gas (C_2N_2) also have specially poisonous effects.

Ventilation.

In the open air the effects of respiration on the atmosphere cannot be appreciated, but in enclosed spaces, such as houses, rooms, &c., which are occupied by many persons, the air soon becomes appreciably changed by their breathing.

The most important changes are (1) removal of oxygen, (2) increase in carbonic acid, and (3) the appearance of some poisonous materials which, though highly injurious, cannot be determined. The deficiency in oxygen never causes any inconvenience, as it is never reduced below what is sufficient for the saturation of the hæmoglobin. The excess of CO_2 seldom gives any inconvenience, since the air becomes disagreeably fusty or stuffy long before the amount of CO_2 from breathing has reached 0·1 per cent., which amount of pure CO_2 can be inspired without any unpleasantness. It is, then, the exhalations coming from the lungs, and probably skin, some of which must have a poisonous character, that render the proper supply of fresh air imperative.

The difficulty of determining the presence of the poisonous organic materials, makes it convenient to use the amount of CO_2 present in the air as the means of measuring its general purity. For this we must suppose that the relation between the poisonous organic ingredients and the CO_2 is constant.

Air, which is rendered impure by breathing, becomes disagreeable to the sense of smell when the CO_2 has reached the low standard of ·06 or ·08 per cent., that is to say, scarcely twice as much CO_2 as is contained in the pure atmosphere. Supposing that air is unwholesome when its impurities are appreciable by the senses, then, if the animal body be the source of the CO_2, ·06 per cent. of this gas makes the air unfit for use.

An adult man disengages more than half a cubic foot of CO_2 in one hour (·6 Parkes), and consequently in that time he renders quite unfit for use more than 1000 cubic feet of air, by raising the percentage of CO_2 to ·1 (0·4 being initial, and ·06 respiratory).

It is obvious that the smaller the space and the more confined, the more rapidly will the air become vitiated by respiration. It becomes necessary for health, therefore, to have not only a certain cubic space and a certain change of air for each individual, but the cubic space and the change of air should bear to each other a certain proportion in order that the air may remain sufficiently pure.

The space allowed in public institutions varies from 500 to 1500 cubic feet per head in such apartments as are occupied by the individuals day and night. As a fair average 1000 cubic feet may be fixed as the necessary space in a perfect hygienic arrangement. In order to keep this perfectly wholesome and free from a stuffy smell, and the CO_2 below ·06 per cent., it is necessary to supply some 2000 cubic feet of air per head per hour.

To give the necessary supply of fresh air without introducing draughts or greatly reducing the temperature of the room is no easy matter, and forms the special study of the hygienic engineer.

Asphyxia.

If an adequate supply of oxygen be withheld and its percentage in the blood is reduced to a certain point, the death of the animal follows in 3 to 5 minutes, accompanied by a series of phenomena commonly included under the term asphyxia. This may be divided into four stages. 1. Dyspnœa. 2. Convulsion. 3. Exhaustion. 4. Inspiratory spasm. As asphyxia is a mode of death the symptoms of which the physician may be called upon to treat, he should be able to recognise its different phases.

If the air passages be closed completely the respirations become deep, laboured, and rapid. The respiratory efforts are more and more energetic, and the various supplementary muscles are called into play one after the other, until gradually the second stage is reached in about one minute.

As the struggles for air become more severe, the inspiratory muscles lose their power, and the expiratory efforts become more and more marked, until finally the entire body is thrown into a general convulsion in which the traces of a rhythm are hardly apparent. This stage of convulsion is short, the expiratory muscles becoming suddenly relaxed by exhaustion.

Then the longest stage arrives in which the animal lies almost motionless, making some quiet inspiratory attempts. These become gradually deeper and slower, until they are nothing more than deep gasps separated by long irregular intervals.

The pupils of the eyes become widely dilated, the pulse can hardly be felt, and the animal lies apparently dead, when often after a surprisingly long interval one or more respiratory gasps follow, and with a gentle tremor the animal stretches itself in a kind of tonic inspiratory spasm, after which it is no longer capable of resuscitation. This last pulseless stage, to which the term asphyxia is more properly confined, is the most irregular in duration, but always the longest.

The blood of an animal which has died of asphyxia is nearly destitute of oxygen, the hæmoglobin being in a much more reduced condition than is found in venous blood. The first and most obvious effect produced by the circulation of blood so deficient in oxygen is excessive stimulation of the respiratory centre, which causes the extreme and varied actions just described. In the first stage of asphyxia, the venous blood reaching the systemic arterioles affects their muscular walls, exciting the vaso-constrictor mechanism, so as to cause a rapid and considerable rise in blood pressure and consequent distension of the left ventricle. The general constriction of the small arteries may be brought about by the venous blood acting as a stimulus to the cells of the medullary and spinal vaso-motor centres, or more probably it acts as a direct stimulant to the muscle cells of the arterioles themselves. The centres in the medulla which govern the inhibitory fibres of the pneumogastric are also stimulated, and consequently the heart beats more slowly. The increase in arterial tension and the slow beat give rise to distension of the ventricle, which, when a certain point is reached, impedes the working of the heart, and its muscle begins to beat more and more feebly, so that in the third stage the pulse can hardly be felt. The muscular arterioles then become exhausted and relax, the blood pressure falls rapidly, and with the death of the animal it reaches the level of atmospheric pressure. Both sides of the heart and great veins are engorged with blood in the last stage of asphyxia ; the cardiac muscle being exhausted from want of oxygen, is unable to pump the blood out of the veins, or empty its cavities.

Owing to the force of the *rigor mortis* of the left ventricle, and the greater capacity of the systemic veins, the left side is found comparatively empty some time after death, and at *post-mortem* examination the right side alone is found overfilled.

CHAPTER XX.

BLOOD ELABORATING GLANDS.

In the preceding chapters we have seen that the blood undergoes important changes as it courses through the different parts of its circuit. Where it comes in contact with the tissues it yields to them nutrient material for assimilation, and oxygen for their metabolism, and carries away from them some waste products. In the lungs it receives oxygen and gives off carbonic acid. While it flows through the minute vessels of the alimentary tract some of the materials elaborated by the digestion of food are absorbed, and directly added to the blood ; at the confluence of the great veins in the neck the stream composed of lymph and chyle is poured into the blood before it enters the heart, so as to be thoroughly mingled with it on its return from the general circulation. Moreover, in various glands, different substances are used in the manufacture of their secretions.

Thus there is a kind of material circulation, a constant income and output going on in the blood itself as it passes through the different parts of the body. The investigation of the exact changes which take place in the blood in each organ or part is surrounded with difficulty, and in many cases it is quite impossible to ascertain what changes occur. In some parts it may be made out by noting the results produced, or the substance given off or taken up by the blood, as seen in the changes found in the air after its exposure to the blood in the lungs, where we can definitely state that the blood has lost or gained certain materials, and is so far altered. In other parts, such as the muscles or the ductless glands, where no doubt profound changes in the blood occur, we have no separate outcome which we can analyse, and we must therefore trust altogether for the elucidation of the change going on in them to the differences which may be

found to exist in the blood flowing to, and that flowing from, such an organ. For this purpose one can either examine samples of the blood from the artery and vein of the organ, while the ordinary circulation is going on, or, immediately after the removal of the organ, by causing an artificial stream of blood to flow through it; then the changes brought about in the blood in its passage through the organ will give the required information. It can be seen from the foregoing enumeration of processes, that some organs have a double function as regards the blood. Thus, in the lung there is both renovation by taking in oxygen, and purification by getting rid of carbon dioxide. The textures in their internal respiration take the nutriment and oxygen, and give the blood CO_2 and various other waste products of tissue change.

Ductless Glands.

There is a certain set of organs, which have but slight traits of resemblance to one another, and in consequence of the want of more accurate knowledge as to their exact function, and the fact that they do not pour their products into ducts but probably into the blood current, are commonly grouped together as *ductless* or *blood glands.*

It has been shown that a great part of the absorbed nutrient material passes through a special set of vessels called the lacteals or lymphatics, and in so doing has to traverse peculiar organs called *lymphatic glands*, where it is no doubt modified, and has added to it a number of cells (lymph corpuscles) which subsequently are poured into the large veins with the lymph and become important constituents of the blood.

Some of these blood glands are doubtless nearly akin to the lymphatic glands already described (fig. 151), their duty being the further elaboration and perfection of the blood. In this group are commonly placed the supra-renal capsules, the thyroid, the thymus, and the spleen.

Supra-renal Capsule.

With regard to the function of the supra-renal capsule we may say that nothing definite is known. The cortical part is said to resemble the lymph follicles in structure, while the central part, on account of

its numerous peculiar large cells, and great richness in nerves, has been explained as belonging to the nervous system.

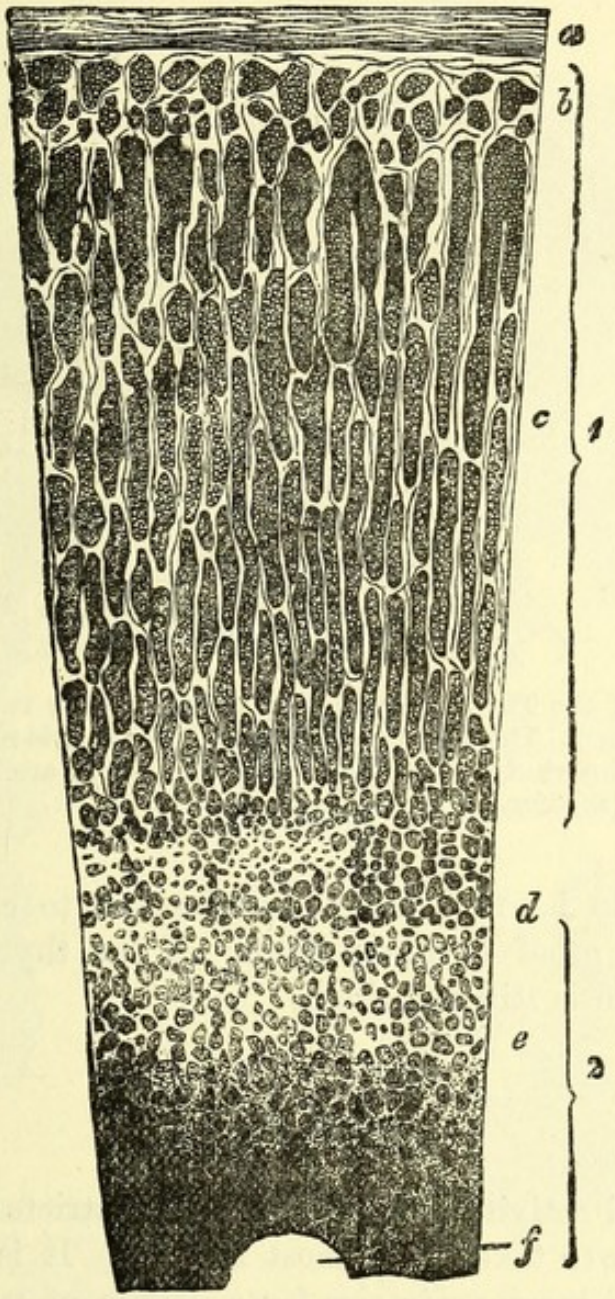


Fig. 156.—Vertical section of the Supra-renal Capsule. (Eberth.)
1. Cortex. 2. Medulla.
a. Fibrous capsule.
b. External cell masses.
c. Columnal layer.
d. Internal cell masses.
e. Medullary substance, in which lies a large vein, partly seen in section *f*.

Thyroid Body.

The thyroid is made up of groups of minute closed sacs embedded in a stroma of connective tissue, lined with a single row of epithelium

cells, and filled with a clear fluid containing mucin. In the adult the sacs are commonly much distended with a colloid substance and peculiar crystals, and the epithelium has disappeared from their walls.

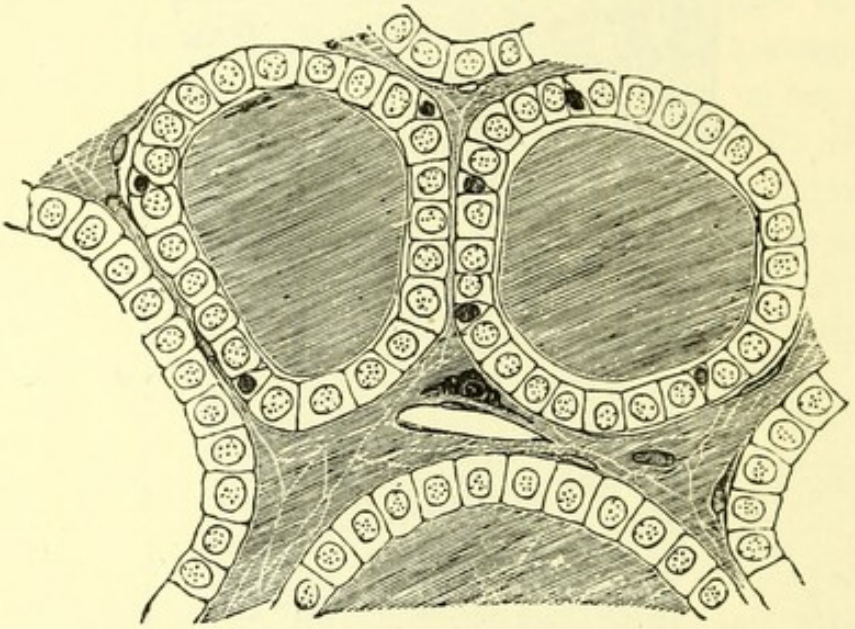


Fig. 157.—Section of the Thyroid Gland of a child, showing two complete sacs and portions of others. The homogeneous colloid substance is represented as occupying the central part of the cavity of the vesicles, which are lined by even cubical epithelium. (Schäfer.)

Although said to be rich in lymphatics and to contain follicular tissue, positive proof of the relation of the thyroid body to the lymphatic system is still wanting.

Thymus Gland.

The functional activity of the thymus is restricted to that period of life when growth takes place most rapidly. It is well developed in the fœtus, and increases in size for a couple of years after birth; but it gradually diminishes in bulk and loses its original structure during the later periods of childhood, so as to become completely degenerated and fatty in the adult. It is composed of numerous little follicles of lymphoid tissue collected into groups or lobules connected to a kind of central stalk. The lymphoid follicles of the young thymus have some likeness to those of the intestinal tract, but they differ from these agminate glands not only in arrangement but also in having peculiar small nests of large cells (corpuscles of Hassall) in the midst of the adenoid tissue of which they are made up. On account of the structure of the lobules being

so nearly identical with that of a lymphatic gland, and from its great richness in lymphatic vessels, the thymus is said to be related to the

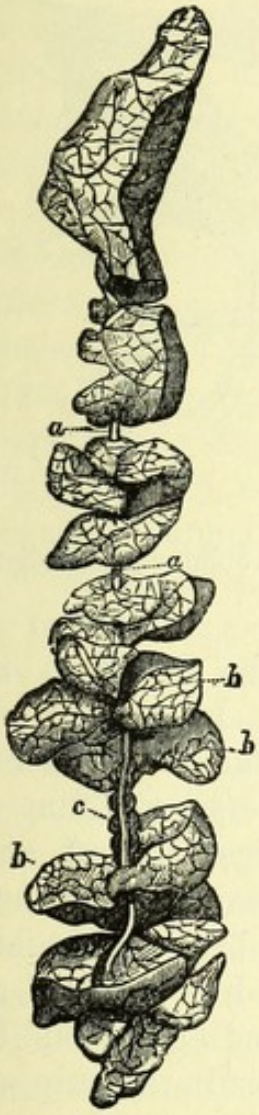


Fig. 158.—Portion of Thymus removed from its envelope and unravelled so as to show the lobules (*b*, *b*) attached to a central band of connective tissue (*a*).

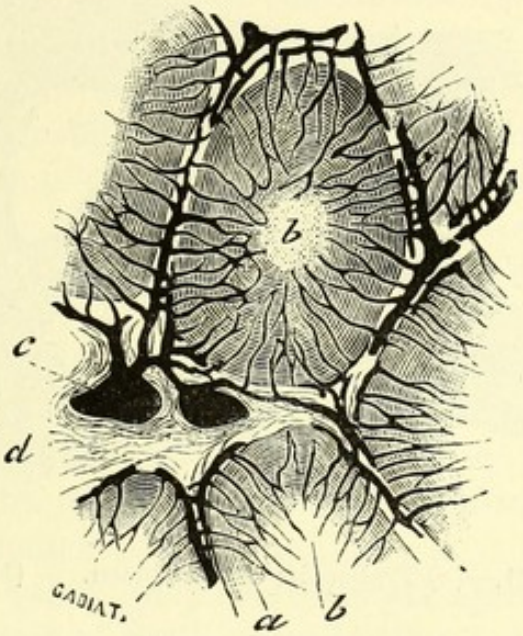


Fig. 159.—Magnified section of a portion of injected Thymus, showing one complete lobule with soft central part (cavity) (*b*), and parts of other lobules. (Cadiat.)
(*a*) Lymphoid tissue. (*c*) Blood vessels. (*d*) Fibrous tissue.

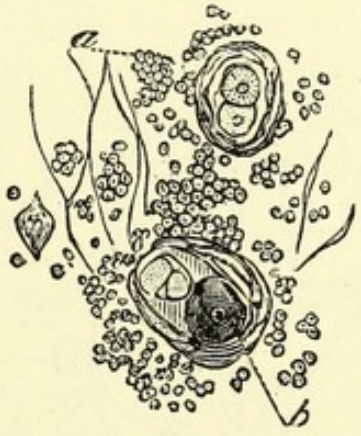


Fig. 160.—Elements of Thymus (high power). (Cadiat).
(*a*) Lymph corpuscles.
(*b*) Epitheloid nests of Hassall.

lymphatic system, and is supposed to play an important part in the elaboration of the blood during the earlier stages of animal life.

SPLEEN.

Structure.—The spleen also resembles a lymphatic organ in structure, but differs from it in the relation borne by the blood to

the elements of the follicular tissue. It is incased in a strong capsule made of fibrous tissue and unstriated muscle cells. From

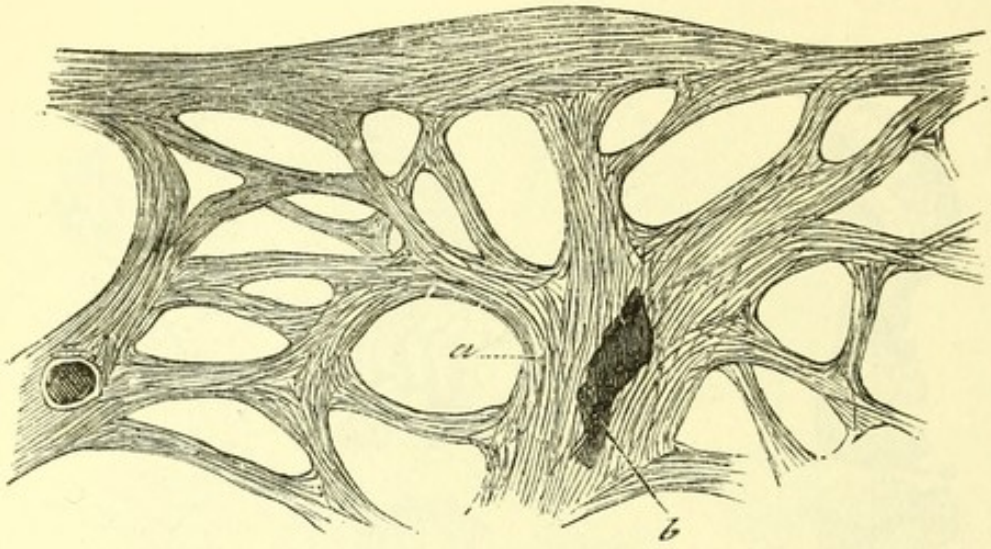


Fig. 161.—(*a*) Trabeculæ of the Spleen. (*b*) Artery cut obliquely. (Cadiat.)

this many branching prolongations pass into the substance of the organ, so as to traverse the soft red spleen pulp. In these trabeculæ or prolongations from the capsule are found the branches of the splenic artery, dividing into smaller twigs without anastomosis. On leaving the trabeculæ the arteries break up suddenly into a brush-like series of small branches, ending in capillaries which are lost in the pulp where the small veins may be seen to commence.

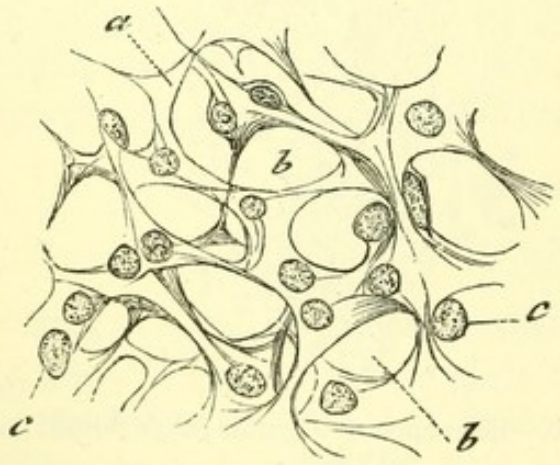


Fig. 162.—Reticulum of the Spleen Pulp injected with colourless gelatine. (Cadiat).
(*a*) Meshes made of endothelium.
(*b*) Lacunar spaces, through which the blood flows.
(*c*) Nuclei of endothelium.

Between the trabeculæ are found two distinct kinds of tissue —(1.) Rounded masses of *lymphoid tissue*, called Malpighian bodies, scattered here and there through the organ ; and (2.) the peculiar soft *splenic pulp* making up its bulk.

The small rounded masses of lymph follicular tissue are situated on the course of the fine arterial twigs. The delicate adenoid reticulum which holds the lymph cells together, is intimately connected with the vessel wall. The pale appearance of these follicles,

which distinguishes them from the surrounding splenic pulp, depends on the number of the white cells which are packed in the meshes of this perivascular adenoid tissue.

The splenic pulp consists of a system of communicating lacunar spaces lined with endothelium. Into these spaces the blood is poured from the arteries, and thus mingles with vast numbers of white cells. Besides the ordinary blood discs and the white corpuscles or lymph cells, many peculiar cells are found in the spleen pulp. Some of these look like lymph cells containing little masses of hæmoglobin, and appear to be transitions from the colourless to the red corpuscles, whilst some small, misshapen, red corpuscles, are regarded as steps in a retrograde change in the discs. But few, if any, lymph channels lead from the spleen-pulp, and only a relatively small number pass out from the hilus, so that the splenic artery and vein must be regarded as taking the place of the afferent and efferent lymph channels.

Chemical composition of the spleen pulp. — Chemical examination shows the splenic pulp to have remarkable peculiarities. Although so full of blood, which is generally alkaline, the spleen is acid in *reaction*, and contains a great quantity of the oxidation products (so-called *extractives*) commonly found as the result of active tissue change. The chief of these are uric acid, leucin, xanthin, hypoxanthin, inosit, lactic, formic, succinic, acetic, and butyric acids. It also contains numerous *pigments*, rich in carbon, but little known, which are probably the outcome of destroyed hæmoglobin. A peculiarly suggestive constituent is an albuminous body containing *iron*. The ash is found to contain a considerable quantity of oxide of iron, to be rich in *phosphates* and *soda*, with but small quantities of chlorides and potassium.

Changes in the blood in the spleen. — If the blood flowing in the artery to the spleen be compared with that in the vein, the difference gives us the changes the blood has undergone in the organ, aud hence is of great importance. In the blood of the vein is found an enormous increase in the number of the white corpuscles (1 white to 70 red in the vein, as against 1 to 2,000 in the splenic artery). The red corpuscles from the vein are smaller, brighter, less flattened than those of ordinary blood; they do not form *rouleaux*, and are more capable of resisting the injurious influence of water. The blood of the splenic vein is also said to have a greater proportion of water, and to contain an unusual quantity of uric acid and other products of tissue waste. The amount of blood in the spleen varies greatly at different times. Shortly after meals the organ

becomes turgid, and remains enlarged during the later periods or digestion.

Pathological changes.—The size of the spleen, which may be taken as a measure of its blood contents, is also altered by many abnormal conditions of the blood. Thus, in all kinds of fever, particularly ague and typhoid, and in syphilis, the spleen becomes turgid, and in some of these diseases it remains swollen for some time. In a remarkable disease, leucocythæmia, in which the white blood cells are greatly increased in number, and the red ones are comparatively diminished, the spleen, in company with the lymphatic glands, is often found to be profoundly altered and diseased, and commonly immensely enlarged; but, on the other hand, advanced amyloid degeneration of the spleen may occur without any notable alteration taking place in the number or properties of the blood corpuscles.

Extirpation of the spleen.—The spleen may be removed from the body without any marked changes taking place in the blood or the economy generally. It is said that if an animal whose spleen is extirpated be allowed to live for a certain time the lymphatic glands increase in size, or become swollen.

In attempting to assign a definite function to the spleen all the foregoing facts must be carefully reviewed, and the peculiarity of its (1) *structure*, (2) *chemical composition*, (3) the *changes the blood* undergoes while flowing through it, (4) the *variations in blood supply* which follow normal and pathological changes in the economy, and (5) the absence of effect following its *extirpation*, must all be borne in mind.

Its *structure* teaches us that it is intimately related to lymphatic glands. The Malpighian bodies are simply lymph follicles, and the pulp may be regarded as a sinus like that of a lymph-gland, with this difference, that it is traversed by blood instead of lymph. The cell elements found in it indicate that not only white cells are rapidly generated, but also that these cells have some peculiar relationship to hæmoglobin, as they are often found to contain some. The varieties in size, form, and general appearance of the red corpuscles can be accounted for by either their destruction or their formation occurring in this organ.

Its *chemical composition* also shows that certain special changes go on in the pulp, and that probably stages of the construction or destruction of hæmoglobin are here accomplished may be inferred from the peculiar association of iron with albuminous bodies.

From the characters of the *blood* flowing from the spleen it has been argued that, besides an enormous production of white corpuscles,

the destruction of the red discs goes on, while some new discs are formed, probably by means of the white cells making hæmoglobin in their protoplasm, which, gradually disappearing, leaves only the red mass of hæmoglobin.

The increased activity of the spleen after *meals*, and in certain *abnormal states* of the blood, as shown by its containing more blood, distinctly points out that some form of blood elaboration goes on in it, which is nearly related to, or associated with, nutrition.

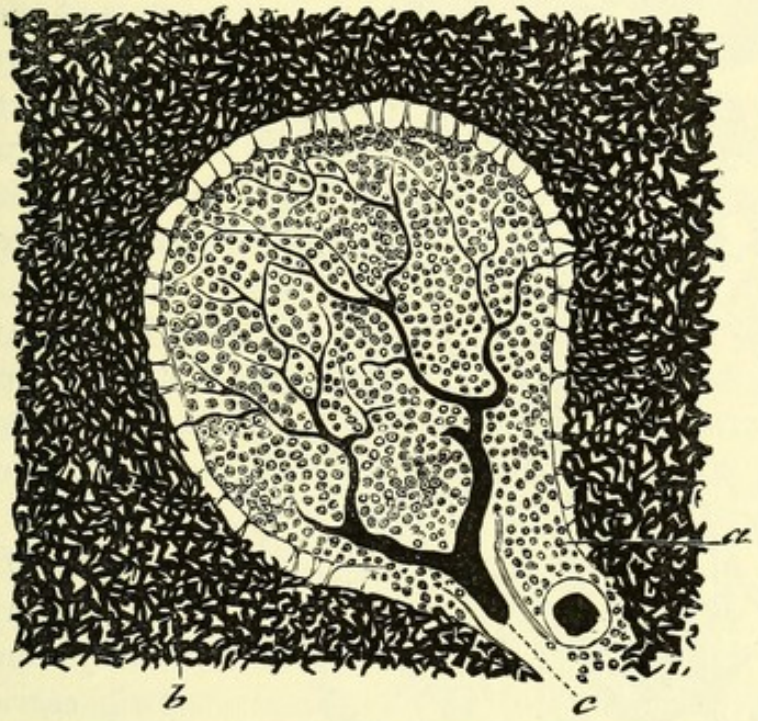


Fig. 163.—Section of Spleen through a lymph follicle (Malpighian body) (*a*) injected to show the vessel, (*c*) entering the follicle, the lymphoid tissue of which is pale in comparison with the pulp (*b*), the meshes of which are filled with injection. (Cadiat.)

The swelling of the lymphatic glands after *extirpation* of the spleen confirms its relation to these organs, and the fact is undisputed that it is a source of the white corpuscles of the blood ; but the paucity of evidence after this operation as to changes in the number or character of the red discs proves that if the spleen be either the place of origin or destruction of the red corpuscles it cannot be the only organ in which they are produced or destroyed.

Glycogenic Function of the Liver.

Of all the organs that modify the composition of the blood flowing through them, the liver plays the most important part in elaborating the circulating fluid. The elimination of the various

constituents of the bile, which has already been mentioned as necessary for the purification of the blood, and useful in aiding absorption, is probably but a secondary function of this great gland. The production of a special material—animal starch—essential to the nutrition and growth of the textures is probably the most important duty of the liver cells, and possibly the constituents of the bile are but the by-products which must be got rid of, resulting from this and other unknown chemical processes.

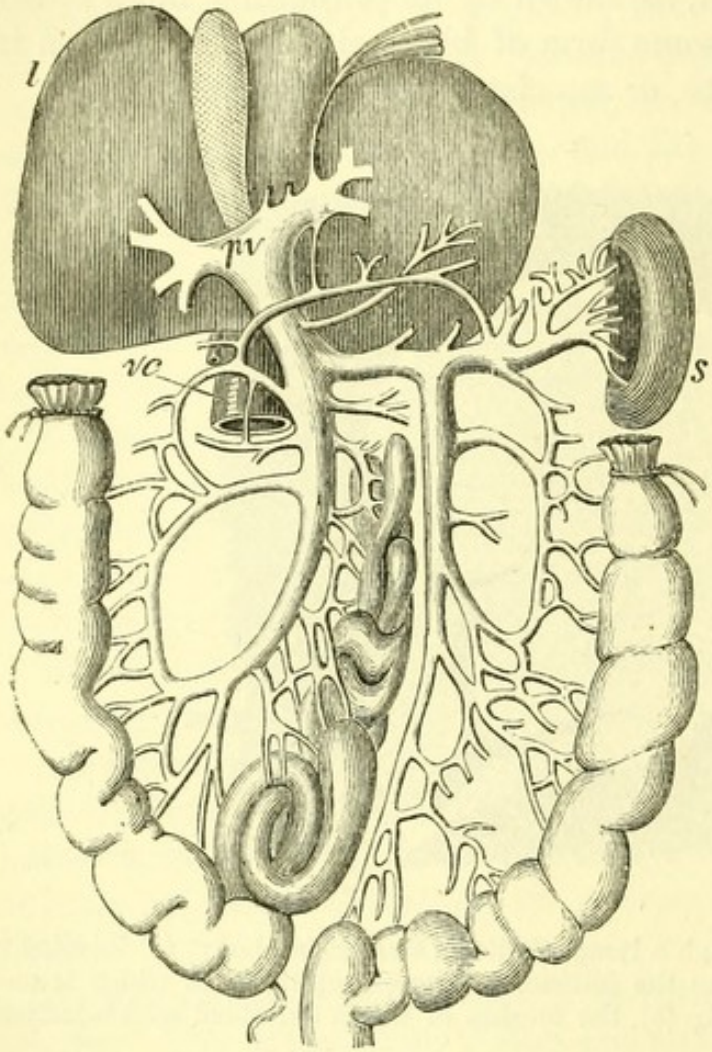


Fig. 164.—Diagram of the Portal Vein (*p v*) arising in the alimentary tract and spleen (*s*), and carrying the blood from these organs to the liver.

In the chapter on the digestive secretions the structure of the liver was mentioned, and attention was directed to the peculiarities of its double blood supply. A relatively small arterial twig carries blood to it from the aorta, while the great portal veins distribute to it all that large supply of blood which flows through the intestinal tract and the spleen.

The blood in the vena porta during digestion can hardly be called venous blood, for much more passes through the intestinal capillaries when digestion is going on than is necessary for the nutrition of the tissue of the intestinal wall. The portal blood is also to be distinguished from ordinary venous blood from the fact that it has just been enriched with a quantity of the soluble materials taken from the intestinal canal, namely, proteids, sugar, salts, and possibly some fats; and it has been further modified by the changes taking place in the spleen.

It is from this blood that the liver-cells manufacture the starch-

like substance above mentioned. Animal starch was discovered by Claude Bernard, and called by him *Glycogen*, on account of the great facility with which it is converted into sugar in the presence of certain ferments which exist in the liver itself and in most tissues after death. Shortly after the death of an animal the tissue of the liver, and also the blood contained in the hepatic veins, are extremely rich in sugar, which has been formed by the fermentation of the hepatic glycogen. The quantity of sugar increases with the length of time that has elapsed since the death of the animal, and is minimal, if not nil, if the liver or hepatic blood be taken for examination while the tissue elements are still alive.

The peculiar blood of the great portal vein coming from the stomach, intestines, and the spleen, has then to pass through a second set of capillaries in the liver, and undergoes such important changes that this organ must be regarded as occupying a foremost position among the blood glands. Differences of the utmost importance have long been thought to exist between the blood going to and that coming from the liver, and to it has even been attributed paramount utility as a blood elaborator; but the scientific knowledge of its power in this respect must date from the discovery of its glycogenic function.

Glycogen.

Glycogen is a substance nearly allied to starch in its *chemical composition*, and is converted with great readiness into grape-sugar by the action of certain ferments and acids. Many of the animal textures contain these ferments, among others the liver itself, at least when its tissue is dying; and consequently the liver with the blood coming from it (if examined in an animal some time dead) does not contain glycogen, but sugar which has been formed from it. If a piece of liver taken from an animal immediately after it is killed be plunged into boiling water, so as to check the action of the ferment, no trace of sugar is found in it, but only glycogen. After the lapse of a little time another piece of the same liver, which has lain at the ordinary room temperature, will give abundance of sugar.

The *mode of preparation* of glycogen depends upon the foregoing facts. The perfectly fresh liver taken from an animal killed during digestion is rapidly subdivided in boiling water. When the ferment has been destroyed by heat the pieces of liver are rubbed up to a pulp in a mortar, and then re-boiled in the same fluid. The liquor is then fil-

tered, and from the filtrate the albuminous substances are precipitated with potassio-mercuric iodide and hydrochloric acid, and removed on a filter. From this filtrate the glycogen may be precipitated by alcohol, caught on a filter, washed with æther to remove fat, and dried.

Glycogen thus prepared has the following *properties*. It is a white powder, forming an opalescent solution in water, which becomes clear on the addition of caustic alkalis. It is insoluble in alcohol and æther. With a solution of iodine it gives a wine-red colour, and not blue, like starch, which it otherwise much resembles in chemical relationship.

Glycogen is widely *distributed* among many other parts besides the liver, namely, in all the tissues of the embryo, and in the muscles, testicles, inflamed organs, and pus of adults ; in short, where any very active tissue change or growth is going on, some traces of glycogen can be found.

Some light is thrown upon its *origin* by the fact that the amount of glycogen in the liver depends in a great measure on the kind and quantity of food used. It rapidly increases with a full, and decreases with a spare diet, though it never disappears even in prolonged starvation. The formation of glycogen is much more dependent on the carbo-hydrate food than on the proteid, for it rapidly rises with increase in the quantity of sugar taken, and falls, as in starvation, when pure proteid (fibrin) without any carbo-hydrate is used either with or without fat. Although the large supply of glycogen normally manufactured in the liver is probably derived from the sugar of the food, we must not conclude from this that the liver cells cannot make glycogen from other materials. Possibly anything that suffices for the nutrition of their own protoplasm enables the cells to produce glycogen. The slowness with which glycogen disappears in starvation would seem to point to this.

The ultimate *destiny* and physiological application of glycogen have been for some time vexed questions. Whether it is converted into sugar, and as such carried off by the blood to the tissues, or whether it is simply distributed as glycogen, is disputed by different observers, while others say glycogen is a step in the formation of fat out of carbo-hydrate.

The want of clear evidence on the subject, together with the obvious chemical difficulties, force us to abandon the theory that fat can be an immediate outcome of liver glycogen, though we must admit that carbo-hydrates, or any form of nutriment, may indirectly aid in the ultimate formation of fat by protoplasm.

The difficulty of determining the exact amount of sugar or glycogen in the blood makes this a very unsatisfactory means of determining the physiological application of liver glycogen. It seems probable that glycogen forms the general carbo-hydrate nutriment of the textures. The diffusible sugar being transformed in the liver, into indiffusible glycogen, in order that it may be distributed throughout the various tissues without being lost in the excretions.

CHAPTER XXI.

SECRETIONS.

The secretions which are poured into the alimentary tract have been already described in the chapter on digestion. There are other glands which can now be conveniently considered since they more or less alter the blood flowing through them, and thus may be said to aid slightly in the perfect elaboration of that fluid. They are, however, subservient to very different functions; some having merely local offices to perform, and others having duties allotted to them of the greatest general importance to the economy. This becomes obvious from a glance at the following enumeration of the remaining glandular organs.

Secreting glands (other than those forming special digestive juices):—

Lachrymal.
Mucous.
Mammary.
Sebaceous.

Excreting glands:—

Sudorific.
Urinary.

SURFACE GLANDS.

Lachrymal Glands.

Most vertebrate animals that live in air have a gland in connection with the surface of their eyes, which secretes a thin fluid to moisten the conjunctiva. This fluid commonly passes from the eye into the nasal cavity, and supplies the inspired air with moisture.

The lachrymal fluid is clear and colourless, with a distinctly salty taste and alkaline reaction. It contains only about 1 per cent. of solids, in which can be detected some albumin, mucus, and fat (1 per cent.), epithelium (1 per cent.) as well as sodium chloride and other salts (·8 per cent.).

The secretion is produced continuously in small amount, but is subject to such considerable and sudden increase, that at times it cannot all escape by the nasal duct, but is accumulated in the eyes, until it overflows to the cheek as tears. This excessive secretion may be induced by the application of stimuli to the conjunctiva, the lining membrane of the nose, or the skin of the face, or by strong stimulation of the retina, as when one looks at the sun. A similar increase of secretion follows certain emotional states consequent on grief or joy. These facts show that the secretion of the gland is under nervous control, the impulses stimulating secretion commonly starting either from the periphery, and passing along the sensory branches of the fifth or along the optic nerve, or from the emotional centres in the brain, and arriving at the gland in a reflex manner. The amount of secretion can also be augmented by direct stimulation of the lachrymal nerves, so that in all probability these are the efferent channels for the impulse.

Mucous Glands.

In connection with mouth and stomach secretions, mention has been made of glands which are elongated saccules lined with clear cells with highly refracting contents (Fig. 165). They are distributed over all mucous membranes, and are the chief source of the thick, tenacious, clear, alkaline, and tasteless secretion called mucus.

This material contains about 5 per cent. of solid matters, of which the chief is *mucin*, the characteristic material of mucus, which swells up in water and gives the peculiar tenacity to the fluid. It is precipitated by weak mineral and acetic acids; and, as the precipitate with the latter does not redissolve in an excess, this acid becomes a good test to distinguish it from its chemical allies. Mucin is not precipitated by boiling. Mucus also contains traces of fat and albumin, and inorganic salts, viz., sodium chloride, phosphates and sulphates, and traces of iron.

The fluid is secreted either by the special mucous glands, or it may be produced by the epithelium of the mucous surfaces. The cells produce in their protoplasm a quantity of the secretion, which may often be seen to swell them out to a considerable extent. This clear fluid is then expelled, and the altered cells are repaired or replaced. Many form-elements, like the remains of epithelial cells, are found in the secretion; and also round nucleated masses of protoplasm similar to white blood corpuscles after the imbibition of water. In the abnormal secretion of a mucous surface during inflammation these

mucous corpuscles are, as well as the general amount of secretion, greatly increased, so that the secretion may become opaque, and may appear to be purulent.

The chief object of the secretion seems to be to protect the mucous surfaces, which are rich in delicate nerves and vessels, and are sub-

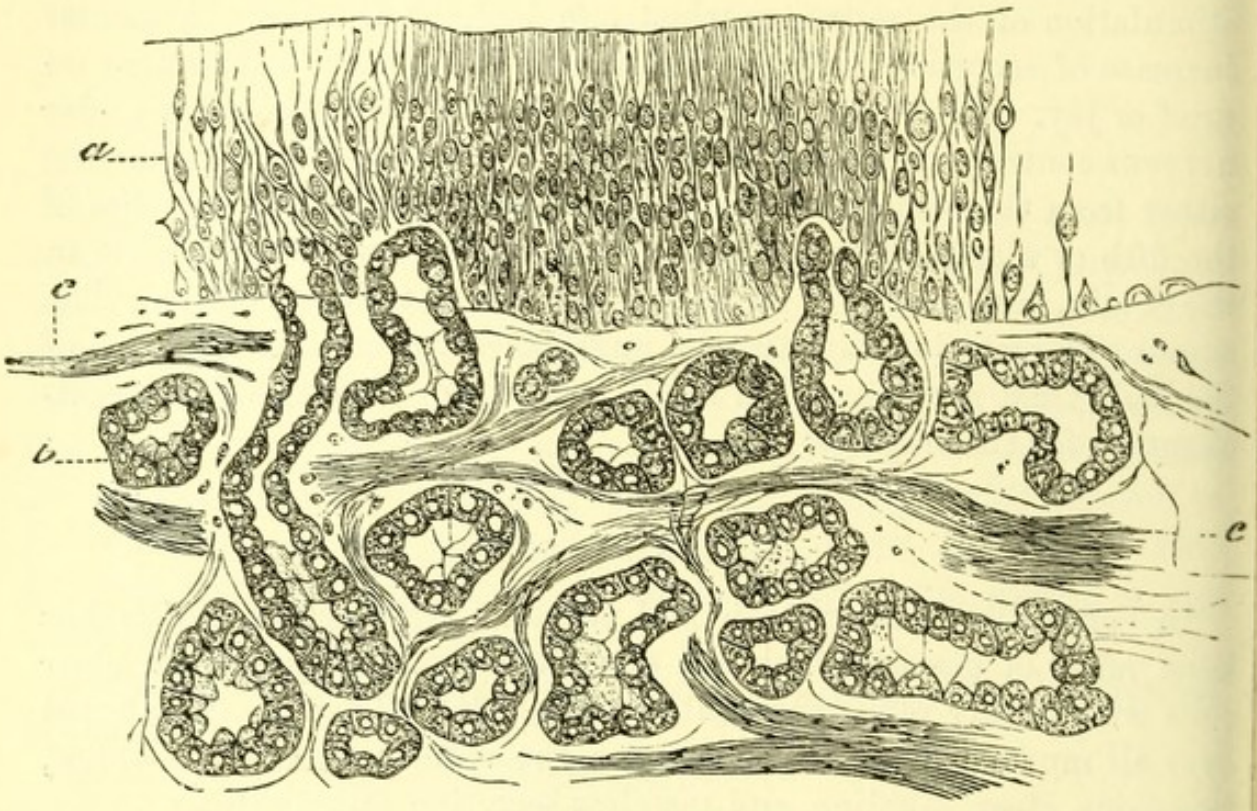


Fig. 165.—Section of the Mucous Membrane of the upper part of nasal cavity showing numerous Mucous Glands cut in various directions. *a*, Surface epithelium; *b*, gland saccule lined with secreting cells; *c*, connective tissue. (Cadiat.)

jected to many injurious influences of a chemical or mechanical nature. It is analogous to the keratin of the epidermis, and may be regarded as an excretion since it is not absorbed, but is cast out from the mucous passages, and passes from the intestinal tract with the fæces, and from the air passages as sputum, &c.

Sebaceous Glands.

These belong to the outer skin, and commonly open into the follicles of the hairs, but also appear on the free surface of the lips and prepuce, &c., where no hairs exist.

The secretion cannot be collected in great quantity in a normal condition, but as far as can be made out, it is composed of neutral fat, soap, and an albuminous body allied to casein, and organic salts and water, about 60 per cent.

The secretion contains the remains of numerous epithelial

cells which are thrown off from the inner surface of the glands, while they are undergoing a peculiar kind of fatty change. These cells gradually get quite broken down during their sojourn in the gland alveoli, and the secretion is finally pressed out by the band of smooth muscle which usually embraces the gland and squeezes it against the hair follicle.

This secretion, the use of which is to lubricate the surface with a fatty material, is cast off with the desquamated epithelium and the

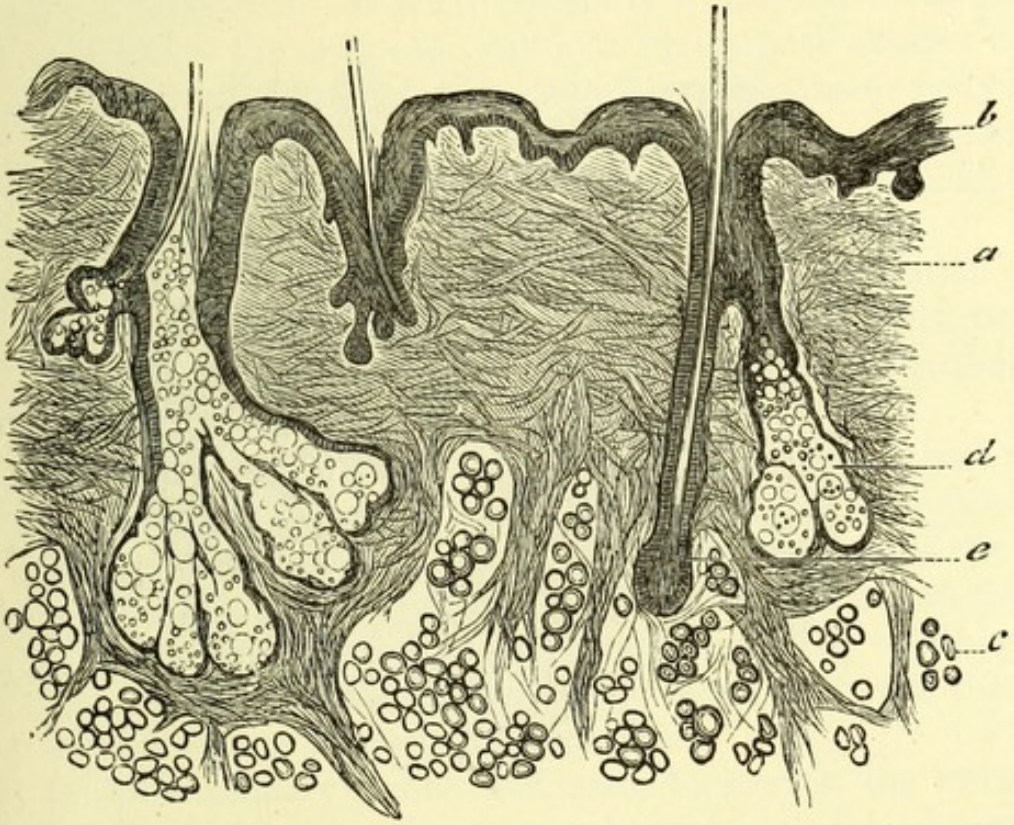


Fig. 166.—Section of Skin showing the roots of three hairs and two large sebaceous glands (*d*). (Cadiat.)

aairs. The Meibomian glands of the eyelids are analogous structures, and are specially elaborated for the lubrication of the ciliary nargin. The glands about the prepuce and clitoris are also analogous o the sebaceous glands; in some animals (Castor) they secrete a peculiarly odoriferous material.

Mammary Glands.

The secretion of milk only takes place under certain circumstances, nd continues for a limited period. As the name of the glands nplies, they are present in all mammalian animals. The activity

of the gland commences in the later stages of pregnancy, and then continues, if the secretion be regularly withdrawn from the gland, for some 9 to 12 months.

During pregnancy the breasts undergo certain preparatory changes prior to the appearance of the milk. They increase in bulk owing to the greater blood supply, and to certain changes in the cell elements of the glands, which are compound saccular glands. Each breast contains a series of some ten to twelve glands with distinct ducts; upon

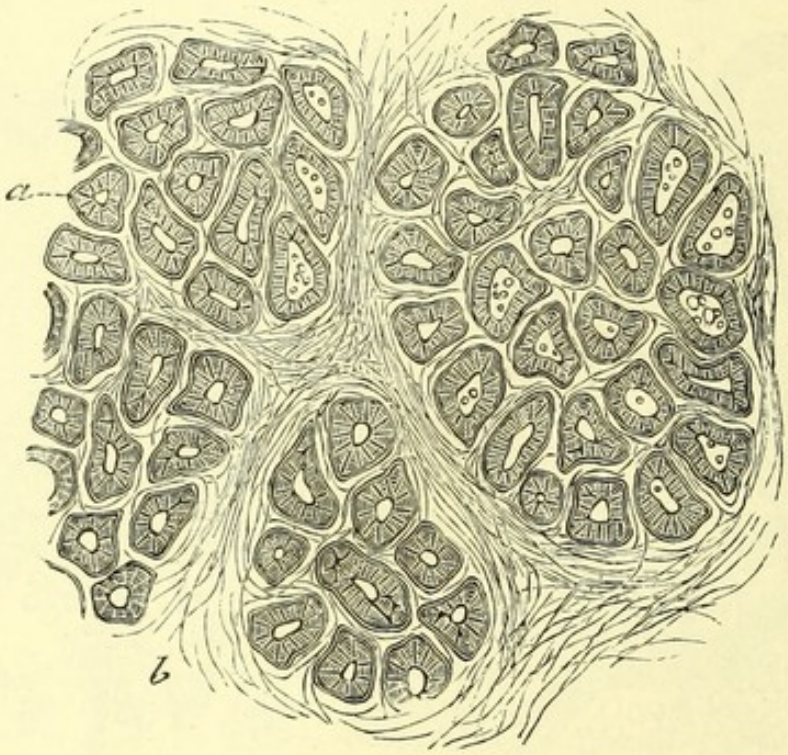


Fig. 167.—Section of Mammary Gland during active lactation (human).
(*a*) Saccules lined with regular epithelium.
(*b*) Connective tissue between the alveoli. (Cadiat.)

these there are dilatations that act as reservoirs in which, during active lactation, the secretion is stored until needed.

The alveoli are chiefly saccular in form, and are lined with a single layer of glandular epithelium, and, during active lactation, contain but little fat, though in the later stages of pregnancy before the secretion is established the cells contain quantities of large fat globules.

Milk.

Milk is a yellowish-white, perfectly opaque, sweetish fluid, with an alkaline reaction and a specific gravity of about 1030. When exposed to the air, particularly in warm weather, the milk soon loses its alka-

linity, first becoming neutral, and subsequently acid ; the milk is then said to have "turned sour," but its appearance is not greatly changed. When it has stood a very long time it may crack or curdle, and separate into two parts; one a thick white *curd* and the other a thin yellowish fluid. This turning sour and ultimate curdling depends upon a change brought about in one of its most important constituents, namely, milk sugar, by means of a process of fermentation. The milk sugar, in the presence of certain forms of bacteria, ferments and gives rise to *lactic acid.* When the quantity of lactic acid is sufficient, it not only makes the milk sour, but also precipitates another of its important constituents, namely, casein. This albuminous body in its coagulation entangles the fat of the milk, and we have thus formed the curd of cracked milk, whilst the whey consists of the acid, salts, and remaining milk sugar.

Although the curdling of milk depends on the coagulation of an albuminous body, it is never produced by boiling fresh milk, because the chief proteid is *casein,* a form of derived albumin (alkali-albumin), which does not coagulate by heat.

When milk is preserved from impurities and kept in a cool place, a thick yellow film soon collects on the top of the fluid, the thickness of this layer—the *cream,* may be taken as a rough gauge of the richness of the milk. Milk consists of a fine emulsion of fat, the suspended particles of which are kept from running together by a superficial coating of dissolved casein. When left at rest, the light fatty particles float to the top and form cream.

When the mammary glands commence to secrete, the milk contains numerous peculiar structural elements which subsequently disappear from the secretion, but which are of considerable interest in relation to the physiological process of the secretion. These are the *colostrum corpuscles,* which consist of large spherical masses of fine fat-globules held together by the remains of a gland cell, which encloses the fat-globules as a kind of sac or case, and in which at times a nucleus can be made out.

Chemical Composition.

The most remarkable point about the chemical composition of milk is the large proportion of proteid and fat it contains, this renders it unique among the secretions. There are two distinct albuminous bodies present, viz. : *casein*, which appears identical with alkali-albumin, and another form of albumin allied to *serum-albumin.* The

fats are present in the shape of globules of various sizes, being in the condition of a perfect emulsion as above stated. They consist of glycerides of palmitic, stearic, and oleic acids.

The milk sugar is very like glucose or grape sugar, but not so soluble. It has the peculiarity of undergoing lactic fermentation.

Of the inorganic constituents of milk the most important are phosphates and carbonates of the alkalis, *i.e.* the salts required to form bone. It is a remarkable fact that the potash compounds, which are the most abundant in the red blood corpuscles, are present in greater quantity than those of soda.

The following table shows the composition of human milk, a comparison of which with that of some domestic animals will be found on page 69 :—

Casein . .	39·24	
Fat	26·66	
Milk sugar . .	43·64	
Salts . . .	1·38	
		110·92
Water		889·08
		1000·00

The relative quantity of the several ingredients of milk varies with the kind of diet used. A vegetable diet increases the per-centage of sugar, but diminishes that of the other constituents, and also the general quantity of milk. A rich meat diet increases both the general quantity and the per-centage of fats and proteids.

The quantity of milk secreted in the twenty-four hours is extremely variable in different individuals, and under different circumstances in the same individual ; the average in general being about two pints.

The amount of the different materials in milk varies under the following rules. The proportion of albumin increases as the milk sugar decreases, and the fat remains the same as the period of lactation advances. The portions of milk last drawn are much richer in fats than that which is first taken from the gland. In the evening the milk is richer in fat than in the morning. The general amount of solid constituents falls, up to the age of thirty years, then gains slightly until thirty-five, after which age the milk becomes decidedly thinner. These points should be borne in mind, as a knowledge of them may prove useful in the selection of a wet-nurse.

Mode of secretion.—Although the blood contains albumins, fats, &c.,

very similar to those which form the solid parts of the milk, we have good reason for thinking that the constituents of milk are not merely extracted from the blood, but that the manufacture of this valuable secretion is due to the activity of the protoplasm of the gland cells, which construct the various ingredients out of their substance.

It has been suggested, as a simple explanation of the formation of milk, that the cells undergo fatty degeneration, and the secretion is then only the debris of the degenerated cells.

Some facts support this view. In the first place the ingredients one finds in milk are suggestive of, though not identical with, the

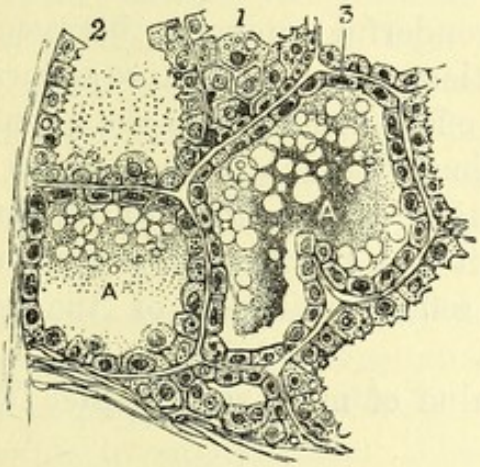


Fig. 168.—Section of the Mammary Gland of a Cat in the early stages of lactation.
(A) Cavity of alveoli filled with granules and globules of fat.
1, 2, 3. Epithelium in various stages of milk formation.

Fig. 169.—Cells of Mammary Gland during lactation, stained with osmic acid so as to show the various sized oil globules as black masses. (Cadiat.)

chemical materials which can be obtained from protoplasm by chemical disintegration rather than of any group of substances found in the blood. Further we find that the so-called colostrum corpuscles, which appear to be secreting cells filled with fat particles, are thrown off from the gland in the early stages of the secretion, and appear in numbers in the milk.

But these colostrum corpuscles soon cease to be thrown off in the secretion, and the saccules of the glands during active lactation do not contain any signs of the debris of cast off cells, or any gradations in degeneration. Only one row of finely granular cells is found lining the saccules, and the cavities are filled with globules of various sizes. From this it would appear that in the earlier stages of the production of the secretion, the mammary cells, after a long period

of inactivity are so unaccustomed to the duty they are called upon to perform, that they succumb in the effort, and, being unable to produce the rich secretion and retain their vitality, they are cast off. Their offspring, however, after a generation or two acquire the necessary faculty of making within their protoplasm all the necessary ingredients of the milk, and discharge them into the lumen of the saccules without themselves undergoing any destructive change.

The composition of the milk teaches us that the cells of this gland can manufacture from their own protoplasm casein, fat, milk sugar, &c., which fact shows beyond doubt that these complex materials may be made in the body.

The *influence of the nervous system* on the secretion of the mammary glands is distinctly shown by the wonderful sympathy between the action of these glands and the conditions of the generative apparatus. Further, different emotions have an effect, not only on the quantity, but also on the quality of the secretion. Local stimulation also promotes the secretion, for the application of the child to the breast at once produces this effect, partly, it may be, through mental influences, but chiefly, no doubt, by reflex excitation of the gland following the local stimulation.

For the details of the dietetic value of milk, see Chapter V. on Food, p. 69.

Excretions.

The term excretion is commonly used to denote a gland-fluid the chief constituents of which are manufactured by other tissues, and are of no use in the economy, but, on the contrary, require to be continually removed in order that their accumulation in the blood may not give rise to injurious consequences. These effete matters are the outcome of the various chemical changes in the tissues, whence they are collected by the blood and carried to the glands which preside over their elimination.

The next group of cutaneous glands is commonly arranged among the excretory organs, though its more important function, as will hereafter appear, is to supply surface moisture for the purpose of regulating the temperature.

Sudoriferous Glands.

The *sweat glands* are distributed all over the cutaneous surface, but in some parts, such as the axilla, perineum, &c., they are both more abundant and larger than elsewhere. They are simple tubes extend-

ing in a more or less wavy manner through the skin, and ending in a rounded knot formed of several coils of the tube some way beneath the corium, where they are surrounded by a capillary plexus. The tube is lined with glandular epithelium, and its basement membrane is beset with longitudinally arranged smooth muscle fibres.

The *secretion of sweat* is always going on, though it does not constantly appear as a moisture on the surface, because the amount produced is only just equal to the amount of evaporation that takes place. In this case it is spoken of as *insensible* perspiration. Under certain circumstances the sweat collects on the surface and becomes obvious as liquid—*sensible* perspiration—which bathes the skin, being produced more rapidly than it can be evaporated. The quantity of secretion necessary to become sensible varies with the dryness and heat of the air, that is, with the rapidity with which evaporation takes place. It happens, however, that the very circumstances which tend to assist evaporation also promote the secretion of sweat. Indeed, the effect of great heat and dryness of the air is to increase the cutaneous secretion more rapidly than they increase the capability of evaporation, and therefore when the air is hot and dry and evaporation is going on very actively, we have the secretion of sweat made sensible to our feelings. When dampness is associated with warmth of the atmosphere the sweat collects in large quantities on the skin, for the heat, as we shall see hereafter, aids the secretion, and the damp air impedes the evaporation.

The *quantity* of perspiration given off is considerable, but the wide limits within which the amount may vary render an attempt to express an average in numbers useless. The amount will depend on (1) the temperature of the air, (2) the quantity and quality of fluids imbibed, (3) the amount of heat generated in the body, and it therefore varies directly with muscular exercise. The amount that becomes perceptible to our senses depends on the impediments to evaporation that may exist, as well as on the amount of fluid produced.

The *chemical composition* of sweat varies with the amount secreted. When collected as a fluid by enclosing a part of the body in an impervious sac, it is found to have about 2 per cent. of solid matters, the greater quantity of which is made up of inorganic salts, sodium chloride being by far the most abundant. It also contains some epithelial debris, traces of neutral fats, and several volatile and fatty acids (butyric, proprionic, caproic), to which it owes its peculiar smell. It is said to contain urea, but this has been denied, and since all the nitrogenous income is accounted for in the urea excreted by the kid-

neys, it is probable that the cutaneous elimination of urea is minimal, if not exclusively pathological. It is also said to contain salts of ammonia, and it affords a means of escape to many drugs. In certain parts of the body, especially in some individuals, it contains a considerable amount of pigments, varying in colour from brick red to bluish-black, which need not be here further described.

The *effect of nervous influence* on the secretion of sweat is so associated with the nervous mechanisms of the cutaneous vessels that under ordinary circumstances it is a difficult matter to separate them. There can be no doubt, however, that a special nervous control is exerted over the production of sweat. This appears to be observable in some diseases, the poisons of which variously affect the two sets of nerves. Thus, in fever, we observe a dry red skin accompanied by an increased supply of blood, and a suppression of the secretion of the sweat glands; whilst in certain stages of acute rheumatism, the exact opposite is seen, *i.e.*, a profuse sweat drips from the pale bloodless skin. It has, moreover, been recently shown that in some animals (cats) the stimulation of the sciatic nerve, causing contraction of the blood-vessels, produces at the same time a copious secretion of sweat; and a warm atmosphere is said to have no effect on the secretion of a limb the nerve of which has been cut, although the warmth be so great as to make the rest of the animal's body sweat profusely.

The *effect of drugs* upon the cutaneous secretion is well known. There is a large group of medicines, especially pilocarpin, which produce an increased flow, while many others, notably atropin, have a contrary effect.

Cutaneous Desquamation.

Together with cutaneous excretion should be mentioned the continuous and extensive loss all over the surface of the body from the casting off of the superficial layers of the dried horny cells of which the outer part of the skin is composed.

The way in which the cells of the mammary gland produce their important secretion is by their protoplasm adopting a peculiar method of fat manufacture, whilst all the strength of its nutritive powers is devoted to the elaboration of the constituents of milk. In a similar way the cells of the epidermis devote their nutritive activity to the production of a certain material—keratin, which cannot be called a secretion in the ordinary acceptation of the term, but which is certainly elaborated as the result of the nutritive changes going on in the protoplasm of the cell during its life-history, just as many other

substances are produced as the result of the nutritive activity of gland cells.

The work of the epidermal cells supplies—not a peculiar chemical re-agent, as do some of the gland cells of the digestive tract, nor yet a nutrient fluid like milk—but an insoluble, impervious, tough coating, for the exterior of the body, which, though thin and elastic, is very strong and resisting.

The nearest analogy among the secretions to the keratin in the epidermal cells, is the production of mucin in the cells of the epithelial lining of the mucous membranes. Both substances may be looked upon as excretions, as they do not re-enter the system, being cast off, but each of them performs a definite function, and is produced by special protoplasmic elements, like the secretions more generally recognised as such.

The amount of nitrogenous substances thus excreted cannot well be reckoned, but having regard to the great extent of surface from which they are derived, it must be considerable.

CHAPTER XXII.

URINARY EXCRETION.

THE urine is the most important fluid excretion, for by it, in mammalia, nearly all the nitrogen of the used-up proteid leaves the body in the form of *urea*. The construction of the urinary glands is peculiar, and requires special notice.

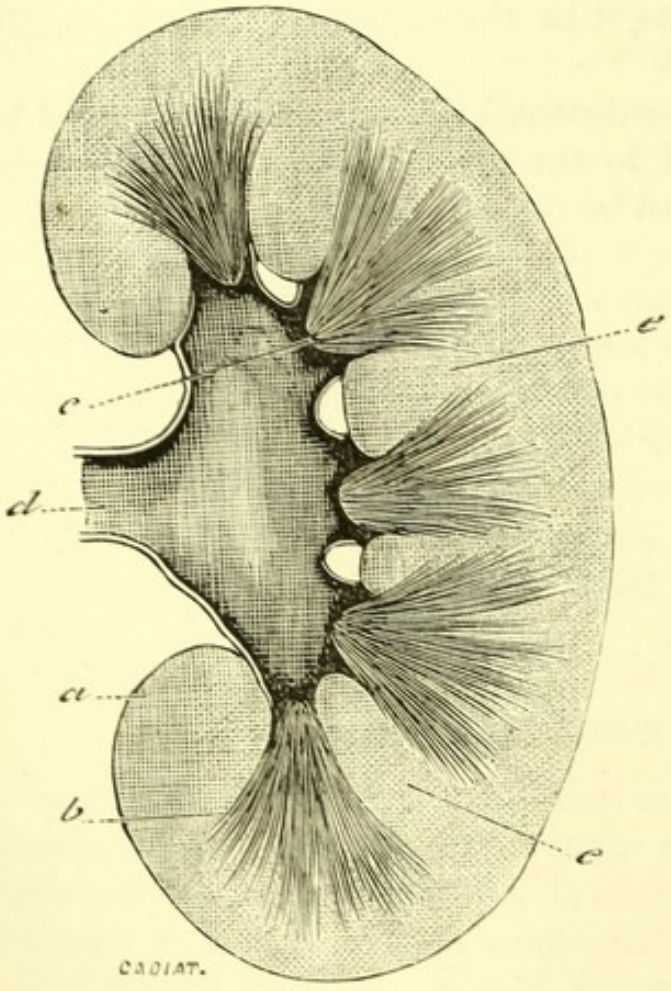


Fig. 170.—Section of Kidney of Man.

a. Cortical substance composed chiefly of convoluted tubules; the portions between the medullary pyramids form the columns of Bertin (*e*).

b. Pyramids of medullary substance, composed of straight tubes, &c., radiating towards cortex.

d. Commencement of ureter leading from central sac or pelvis.

c. Papillæ, where the tubes open into pelvis.—(Cadiat.)

STRUCTURE OF THE KIDNEYS.

The kidneys may be called complex tubular glands, because the tubes of which they are composed are made up of a number of parts essentially differing from one another both in their structure and in their relation to the blood vessels.

The tubes begin by a small rounded dilatation (Malpighian capsule) which is lined by thin flattened epithelium. Opening from this capsule, Fig. 171 (*g*), is found a tortuous tubule (*f*), lined by peculiar large rod-beset epithelial cells, which occupy the greater portion of its diameter. This convoluted

tubule (f) leads into a tube (e) of much less external diameter, but about equal lumen, owing to the thinness of its lining epithelium,

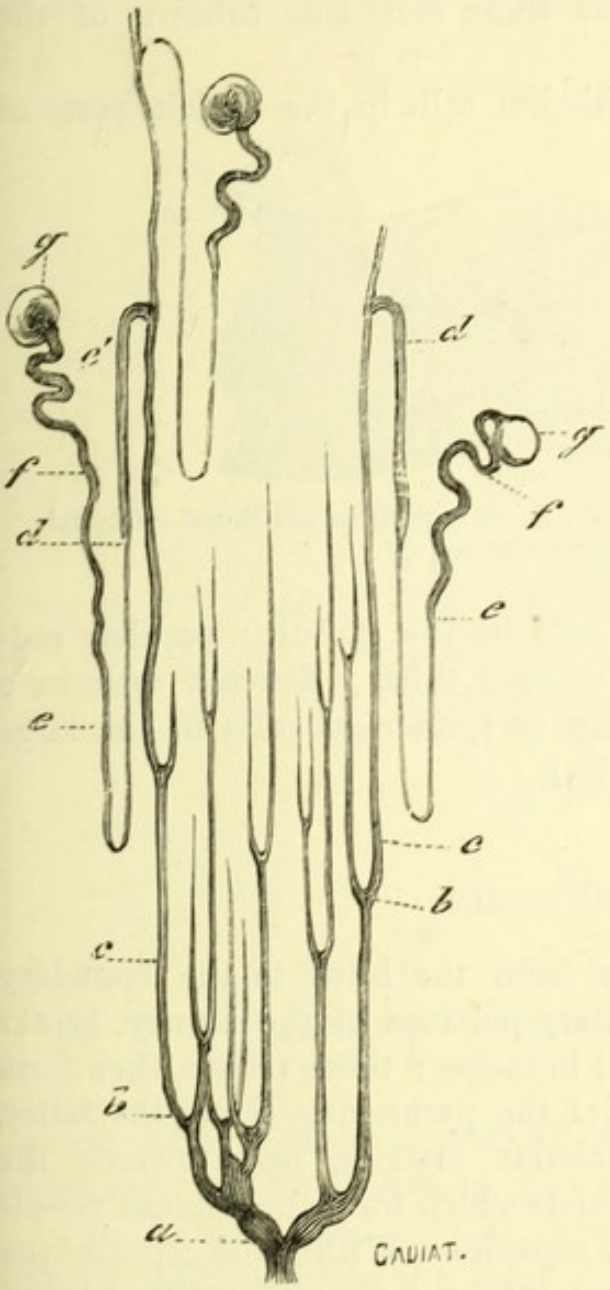


Fig. 171.—Diagram of the Tubules of the Kidney. (Cadiat.)
a. Large duct opening at papilla.
b and *c*. Straight collecting tubes.
d and *e*. Looped tubule of Henle.
f. Convoluted tubules of cortex.
g. Capsule from which the latter spring.

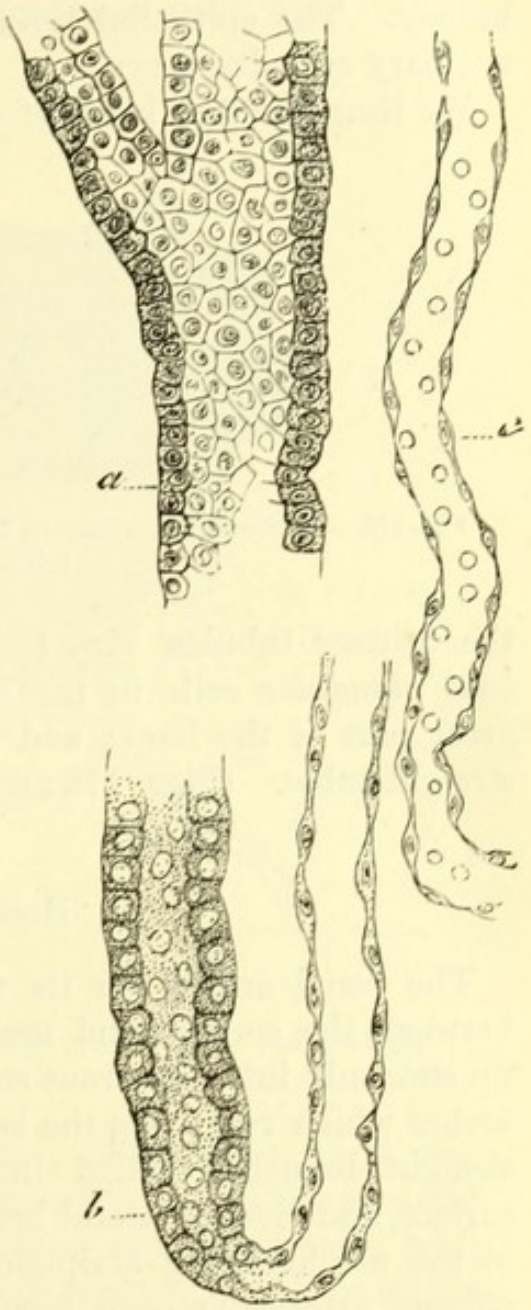


Fig. 172.—Portions of various Tubules highly magnified, showing the relation of the lining epithelium to the wall of the tube. (Cadiat.)
a. Large duct near the papilla.
b. Commencement of Henle's loop.
c. Thin part of Henle's loop.

the cells of which are more flattened and much thinner than those in the tortuous tubes. This thin tube forms a loop extending down to the medullary pyramid and returning to the cortex, where it can be seen to become again convoluted (d) and then to open into a

straight collecting tube. The collecting tubes (*c*, *b*) receive many similar tributary tubes on their way towards the apex of the medullary pyramid, where they pour their contents into the pelvis of the kidney. The epithelial lining of these collecting tubes is of the ordinary cylindrical type.

We thus find four kinds of epithelial cells in the various parts of

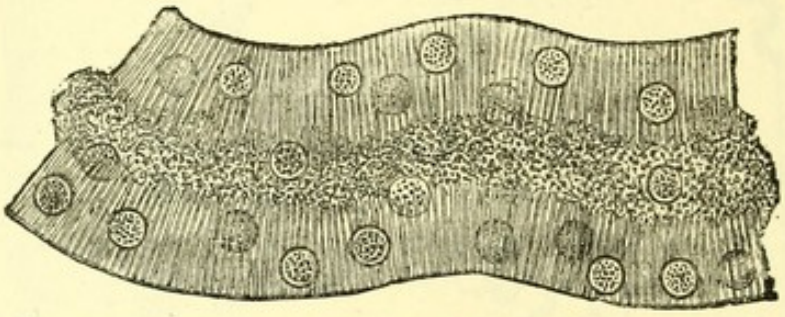


Fig. 173.—Portion of Convoluted Tubule, showing peculiar fibrillated epithelial cells. (Heidenhain.)

the urinary tubules, viz., *scaly* cells in the capsule; peculiar *rod-beset glandular* cells in the convoluted tubes; *flattened* cells in a great part of the loop; and ordinary *cylindrical* cells in the large straight tubes. (Figs. 172 and 173.)

Blood Vessels.

The renal artery, on its way from the hilus to the boundary between the cortical and medullary portions of the kidney, breaks up suddenly into numerous small branches; these vessels then form arches which run along the base of the pyramids. From the latter, straight branches, called interlobular arteries, pass towards the surface, and give off lateral branchlets which form the afferent vessels to the neighbouring Malpighian capsules. Within the capsules the afferent arteries at once break up into a series of capillary loops, forming a kind of tuft of fine vessels—the *glomerulus*, which fills the cavity at the beginning of the tubules, and is only covered by thin, scaly epithelial cells, and thus separated from the urine. It is a singular fact that in the renal circulation the efferent vessel on leaving the glomerulus does not, like most veinlets, unite with others to form a larger vein; but again breaks up into capillaries, which form a dense meshwork around the convoluted tubules. The blood is thence conveyed to small straight veins corresponding to the intralobular arteries.

Another striking peculiarity of the renal vessels is that a distinct

set of arteries, starting from the same point as the interlobular (between the cortex and medulla), pass towards the centre of the gland into the pyramids. They consist of bunches of straight arterioles, which lie between the straight and the looped tubules.

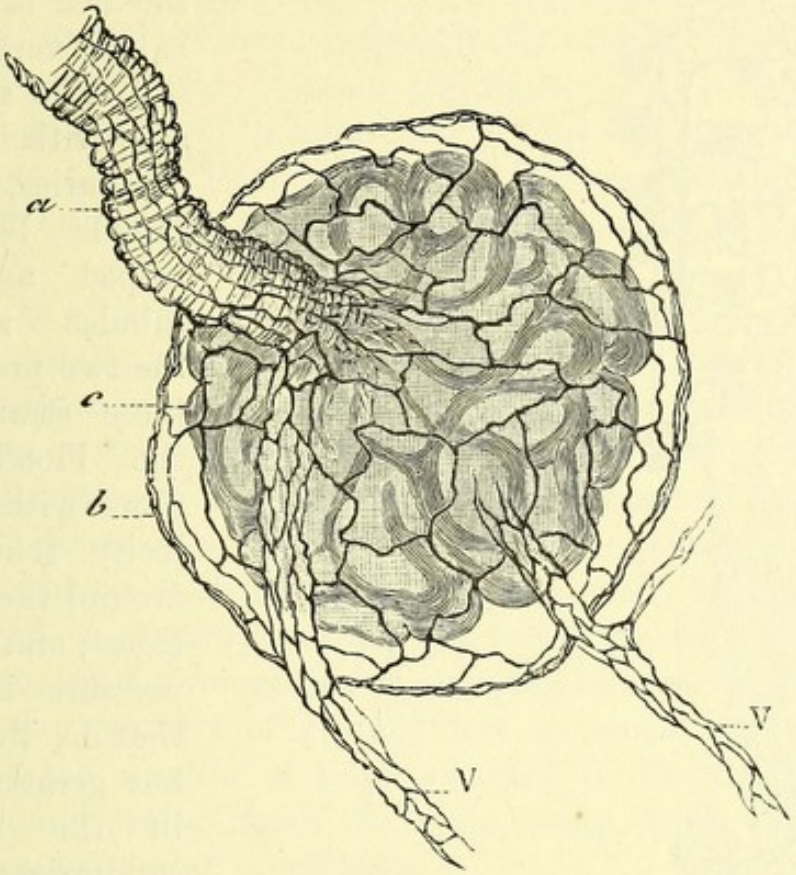


Fig. 174.—Glomerulus, treated with silver nitrate, showing the endothelium.

Corresponding with these straight arteries are minute straight veins, which carry the blood back to the vessels at the base of the pyramids.

In the kidney, then, we have three sets of capillary vessels, which differ in their position, the form of their meshes, and their relation to their parent artery. Probably the pressure exerted by the blood in them, and the rapidity of its flow through them, differ also :—

1. The capillaries in the glomeruli are loops collected into a tuft by their covering of delicate epithelium. On account of their relation to the afferent artery which ends abruptly in these capillaries, and to the smaller efferent vessel that leads to a secondary plexus of capillaries, the pressure within the glomerulus must be very great compared with that of the general capillaries of the body, and must vary much with changes in local blood-pressure.

2. The secondary capillary plexus, with its narrow meshwork

closely investing the tubules, can only be under comparatively trifling pressure which varies but little, on account of the blood having first to pass through the capillaries of the glomerulus. Their current of blood must also move slowly, since the bed of the stream is here very great.

3. The straight vessels, with long meshed capillaries, in the pyramids between the looped and straight tubules are unlike the two preceding. In these straight vessels the blood probably flows with greater velocity than in those around the convoluted tubes; and their blood-pressure is less than that in the glomeruli but greater than that in the intertubular capillaries.

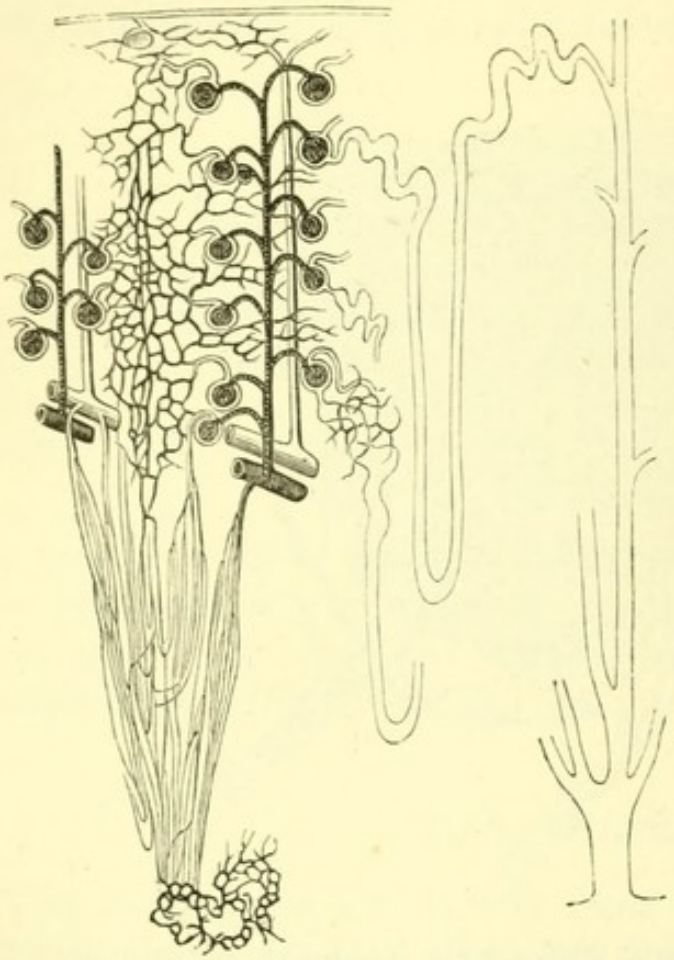


Fig. 175.—Diagram showing the relation borne by the blood vessels to the tubules of the kidney. The upper half corresponds to the cortical, the lower to the medullary part of the organ. The plain tubes are shown separately on the right, and the vessels on the left. The darkly shaded arteries send off straight branches to the pyramid and larger interlobular branches to the glomeruli, the efferent vessels of which form the plexus around the convoluted tubes.

The Urine.

When freshly voided the urine of man in health is a clear straw-coloured fluid, with a peculiar aromatic odour. The intensity of the colour varies with the amount of solids—the colour being a rough indication of the degree of concentration. On standing and cooling a slight cloud of mucus often appears floating in the fluid. This comes from the lining membrane of the bladder, and it usually entangles a few flattened epithelial cells, which are the only organised structural elements found in it in health.

The fresh urine has a distinctly acid reaction. This does not depend upon the presence of free acid, but upon the large amount of

acid salts, particularly acid sodium phosphate, which it invariably contains. A strictly vegetable diet renders man's urine alkaline, and it is said to become less acid after meals. In the herbivorous mammalia the urine is normally alkaline so long as their digestion is going on, but when they are deprived of food for some time it becomes acid, showing that the alkalinity depends upon their diet.

The specific gravity of urine varies greatly at different times, commonly, however, ranging between the figures 1015—1020. After copious drinking, abstinence from proteid food, and in cool weather it may fall as low as 1003, and after prolonged abstinence from liquids, much animal food, and very active sweating, it may attain 1040.

The quantity of urine secreted is also very variable, that produced by an adult usually amounting to about 2 pints per diem (1000—1500 c.c.). The amount is increased by—(1) elevation of the general blood-pressure, or the pressure in the arteries from any cause whatever; (2) contraction of the cutaneous vessels from cold; (3) copious drinking; (4) excess of nitrogenous diet; (5) the presence of soluble matter in the blood, such as sugar, salt, &c.; and, (6), the presence of urea as well as various medicaments, has a special action on the renal secretion, greatly increasing the amount of urine passed.

Although the quantity of urine differs so much under different circumstances, the amount of solids excreted by the kidneys in the 24 hours remains pretty much the same, being on an average over 1½oz. (50 grammes) for an adult man.

From this it is obvious that the height of the Sp. Gr. must vary inversely with the amount secreted, so that the more scanty the urine the higher we expect to find the per-centage of solids.

Secretion of the Urine.

We have just seen that the arterial twig, or *afferent vessel*, which enters the capsule of Malpighi, breaks up into a set of capillary loops, which are only covered by a single layer of extremely thin epithelial cells separating them from the lumen of the urinary tubule, and that the pressure in the vessels of the glomerulus is habitually higher than that in most capillaries, and constantly greater than that of the second capillary network around the convoluted tubules.

The general arrangement of these vessels, and the high pressure in the glomerulus, give the impression that it is simply a filtering apparatus by means of which the fluid parts of the blood pass into

the urinary tubules. This view seems supported by the fact that the quantity of urine secreted bears a direct proportion to the blood-pressure in the minute renal vessels, whether the change in pressure depends on local vascular mechanisms or on changes in the general blood-pressure.

Such a theory, however, cannot adequately explain the formation of urine, because the urine differs so materially from the fluid one could obtain as a filtrate from the blood. In health it contains no albumin, a substance in which the blood is very rich; and it is much richer in urea and salts than the blood. There is, therefore, both a quantitative and qualitative difference, which implies a distinct process of selection, and although filtration may not be altogether excluded from the process, it must be completely modified by other forces.

In the general description of the structure of the organ it was seen that in a great part of the tubules, both the epithelial and vascular supply give the idea of actively secreting gland tubes. From the mere construction of the different portions of the gland, it has been concluded that there are two distinct departments each of which play a different part in the production of the urine. One is said to be a simple filtering mechanism, and the other a definitely secreting glandular tubule.

It is not surprising that, with such a complex arrangement as the tubules above mentioned, there should exist different views as to the exact mode in which the urine is secreted. As these are more or less at variance in their explanation of the method of secretion, and as it is difficult to put any of them aside as quite erroneous, it becomes necessary to enumerate each somewhat in detail.

Feeling convinced of the filter-like function of the glomerulus, and recognising the fact that some other agency was also at work in the formation of urine, Bowman explained the process thus :—From the glomerulus the watery parts of the fluid are filtered, while the glandular epithelium selects the important solid constituents which it is necessary to remove from the blood.

Ludwig takes a different view. He believes that the watery part of the plasma, bearing with it the salts, &c., is filtered from the glomerulus. As this fluid passes through the tortuous urinary tubules, a large portion of the water is re-absorbed into the capillary networks surrounding them. This re-absorption is assisted by the high specific gravity of the blood and the low pressure in these capillaries as compared with those of the glomeruli, where the filtration of the liquid occurs. The *rôle* of the epithelium is not then selection from the

blood of specific materials, but possibly the prevention of the return of the solids with the water back to the blood vessels.

Heidenhain attempted to settle the question as to the function of the renal epithelium, by introducing into the blood a blue colouring matter—pure sodium sulphindigotate—which he found to be eliminated by the kidneys, giving rise to blue urine. On examining the organ with the microscope at a suitable time after the injection of the colour into the blood, the tubules are found to be filled with the pigment, and in some cases the peculiar epithelium of the convoluted tubules is stained with the blue substance, while the glomerulus and capsule are entirely free from the colour. If the stream of fluid from the glomerulus be stopped in any way—tying the ureter, section of the spinal cord, or local destruction of the glomeruli—the blue colour is only to be found in the convoluted tubes and their epithelium, and hence it has been concluded that its presence in the looped and collecting tubes of the kidneys and urinary bladder, depends upon its being washed out of the convoluted tubes by the stream of fluid filtered from the blood at the glomerulus.

The following facts may also be adduced in further support of the view that the glandular epithelium has a considerable share in the removal of the more important solid constituents of the urine.

The epithelium in the tubules of the kidney of birds is found impregnated with acid urates, which form the chief constituents of the solid urine of birds.

The amount of liquid passing out at the kidneys is in direct proportion to the blood pressure, whereas the excretion of the specific constituents of urine is independent of the pressure, but is related to the amount existing in the blood, and the condition of the epithelium. This is shown by the increased elimination of urea when that substance is artificially introduced into the circulation, even after the flow of the fluid has been checked by section of the spinal cord.

Another view has been put forward, which, with some modification, appears plausible, or at least worthy of mention. Paying attention to the fact that where vascular filtration—*i.e.*, the passage of liquid under pressure through the capillary wall—occurs elsewhere in the body it is not only water and salts, but plasma that passes out of the vessels into the interstices of the tissues, we may then assume that the fluid part of the blood, as such, and not merely its watery part, escapes at the glomerulus. That is to say, the solid ingredients of the urine in a diluted form, plus serum-albumin, pass into the tubules. But on its way down the long and circuitous route through the tubules the albumin with much water is re-absorbed by the capil-

laries of the convoluted tubes. The first step in this case is a mechanical filtration; the second is a vital process of re-absorption of a solution of serum-albumin carried on by the gland cells in the tubules, aided by the low pressure in the peri-tubular capillary plexus. This view seems supported by pathological experience, which teaches that the removal of the epithelium of the tubes (the glomeruli remaining perfect), is followed by the appearance of albumin in the urine, and cysts formed by the destruction of the epithelium and occlusion of the tubules, commonly contain a fluid somewhat like plasma.

Doubtless much remains to be found out as to the exact method of secretion of the urine, and possibly future research may show us that all the views here enumerated have some truth in them. That a filtration, not mere osmosis, takes place, seems probable from the special vascular mechanism of the glomerules. Why simply water and salts without albumin should pass through the capillaries of the glomerulus and not through any other capillaries, is not sufficiently explained to make it sure that such a filtration really occurs. That the glandular epithelium does take an active part in the elimination of the urea is rendered almost indisputable from the researches of Heidenhain. And yet there remain other parts, *e.g.*, the loops of Henle, which are invariably found in the kidney, and have a special vascular mechanism, to which none of the foregoing theories assign any special or peculiar function.

From the foregoing evidence we may fairly suppose that most of the urea, and possibly some other solid constituents of the urine, are selected from the blood by the epithelial cells of the convoluted tubules, that the fluid part of the blood escapes at the glomerulus, and flows along the varied and circuitous route of the tubules carrying with it the matters poured into the tubes by the cells, and that in some part of the tubules the dilute filtrate loses much of its water and all its albumin.

Chemical Composition of Urine.

The per-centage of the solid and liquid materials in urine varies as the secretion alters in strength, but on an average it may be said to contain about 4 per cent. of solids and 96 per cent. water.

The following are the more important solid matters :—

Urea is the most important, and at the same time most abundant solid constituent, commonly forming about 2 per cent. of the urine. It is regarded as the chief end-product of the oxidation of the

nitrogenous matter in the body, so that the amount excreted per diem gives us the best estimate of the amount of chemical change taking place in the nutrition of the tissues. It is readily soluble in alcohol and water, but insoluble in ether. It forms acicular crystals with a silky lustre. From a chemical point of view it may be regarded as the monamide of carbamic acid, with the formula $CO\left\{\begin{matrix}NH_2\\NH_2\end{matrix}\right.$. It is isomeric with ammonium cyanate $\left.\begin{matrix}CN\\NH_4\end{matrix}\right\}O$, from which it was first prepared artificially.

On exposure to the air bacteria develop in the urine, and, acting as a ferment, change the urea into ammonium carbonate, two molecules of water being at the same time taken up thus :

$$CO(NH_2)_2+2H_2O=(NH_4)_2CO_3.$$

This gives rise to a change in the reaction of the urine, which after a time becomes increasingly alkaline, and the change is commonly spoken of as the alkaline fermentation of the urine. This change is extremely slow in solutions of pure urea, which do not support bacterial life.

With nitric and oxalic acids, urea forms sparingly soluble salts—a fact made use of in its preparation from urine.

The *amount* of urea eliminated in the 24 hours is about 500 grains (35 grammes). The amount varies (1) in some degree with the amount of urine secreted ; an increase in the amount of water being accompanied by a slight increase in the urea eliminated. Some materials, such as common salt, increase the water, and thereby also increase the urea. (2) The character and quantity of the diet influences most remarkably the quantity of urea given off, the amount increasing in direct proportion to the quantity of proteid consumed. Fasting causes a rapid fall in the amount of urea ; even in the later days of starvation it continues to fall, but very slowly. (3) The amount differs with age, being relatively greater in childhood than in the adult (about half as much again in proportion to the body weight). (4) Many diseases have a marked influence on the amount of urea. In most febrile affections it increases with the intensity of the fever, while in disease of the liver it often notably decreases. In diabetes, if the consumption of food be very great, the daily excretion of urea may reach nearly 4 oz. (100 grammes) or three times as much as normal.

Preparation.—To obtain urea from human urine it is evaporated to one-sixth of its bulk, an excess of nitric acid is added, and it is left to

stand in a cool place. Impure nitrate of urea separates from the fluid as a yellow crystallized precipitate. This sparingly soluble salt is caught on a filter, dried, dissolved in boiling water, mixed with animal charcoal to remove the colouring matter, and filtered while hot; when the filtrate cools, colourless crystals of nitrate of urea are deposited. The precipitate is dissolved in boiling water, and barium carbonate added as long as effervescence takes place, barium nitrate and urea being produced. This is evaporated to dryness, and the urea extracted with absolute alcohol, which on evaporation leaves crystals of pure urea.

Estimation.—Urea can be estimated volumetrically by the method of Liebig, which depends on the power of mercuric nitrate to give a precipitate with it. The sulphates and phosphates must be first removed by the addition of 40 c. c. of a mixture of 1 volume saturated barium nitrate and 2 volumes saturated solution of caustic baryta, to 40 c. c. of urine. This is filtered, and from the filtrate, an amount corresponding to 10 c. c. urine is taken. Into this known volume of urine a standard solution of mercuric nitrate (of which 1 c. c. corresponds to 1 centigramme of urea) is dropped until a sample drop of the liquid, mingled on a watch-glass with a drop of concentrated sodium carbonate solution gives a yellow colour, which indicates that some free mercuric nitrate is present. For every cubic centimetre of the standard mercuric solution used, there is one centigramme of urea in the sample of urine; a reduction of 2 c. c. should be made from the mercuric solution used in the experiment on account of the chlorides, which are present in tolerably constant amount.

Another simple and more accurate method consists in mixing known quantities of urine and sodium hypobromite (NaBrO) with excess of caustic soda. The urea is decomposed in the presence of this salt, and free nitrogen evolved—

$$CON_2H_4+3(NaBrO)+2(NaOH)=3NaBr+Na_2CO_3+3H_2O+2N.$$

The quantity of urea may be determined by ascertaining the volume of nitrogen, which can be measured directly in a graduated tube. 37·5 c. c. of N represents 0·1 gramme of urea at ordinary temperature and pressure.

Uric acid, of which the formula is $C_5H_4N_4O_3$ or $C_3H_2O_3(NH.CN)_2$, is only present in extremely small quantities in the normal urine of mammalia, but in birds, reptiles, and insects it forms the chief ingredient of the renal secretion. It is sparingly soluble in water, and insoluble in alcohol and ether. However, in solutions of the

neutral phosphates and carbonates of the alkalies it combines with some of the base, so as to form acid salts, and at the same time converts the neutral into acid phosphates, to which, as has been already stated, the urine owes its acid reaction. These salts are more soluble in warm than in cold water, and hence generally fall as a sediment when the urine cools. Uric acid is readily converted into urea by oxidation, and is probably one of the steps in the formation of urea generally occurring in the body during the gradual oxidation of the proteid bodies.

The presence of uric acid may be recognised by the murexide test. The substance to be tested is gently heated in a flat capsule with some nitric acid. A decomposition occurs, N and CO_2 going off, urea and alloxan remaining as a layer of yellow fluid. If this be cautiously evaporated, and a drop of ammonia added, a striking purple red colour is produced, which the addition of potash turns violet.

The amount of uric acid normally follows pretty closely the variations in urea, but is usually only about 8 grains (·5 gramme) per diem. In certain diseases the quantity may be much increased. For the quantitative estimation, which is seldom decided by the practitioner, the student must consult the text books of physiological chemistry.

Kreatinin ($C_4H_7N_3O$) is always present in urine, probably being formed from kreatin by the loss of one molecule of water. About 15 grains (1 gramme) is excreted per diem.

Xanthin ($C_5H_4N_4O_2$) also occurs in urine, but in extremely small quantities.

Hippuric acid ($C_9H_9NO_3$) is a normal constituent of human urine, occurring, however, in very small quantities. On the other hand, it is one of the most important nitrogenous constituents of the urine of the herbivora, where it takes the place of uric acid. Its presence depends on the existence of certain ingredients (benzoic acid, &c.) in the food, which are capable of combining with glycin, and forming a conjugated acid, a molecule of water being formed at the same time, thus—

Benzoic Acid.	Glycin.	Hippuric Acid.	Water.
$C_7H_6O_2$	+ $C_2H_5NO_2$	= $C_9H_9NO_3$	+ H_2O.

The amount of hippuric acid increases with increased consumption of vegetable food, in the cellulose of which the materials exist that are required for its formation. The union of glycin and benzoic acid may take place in the liver, for, after removal of that organ, benzoic acid injected into the veins appears unchanged in the urine; but the extirpated kidney is also said to be capable of effecting this synthesis.

Oxalic acid ($C_2H_2O_4$) occurs often but not constantly in the urine. It is generally united with lime. It is said to appear in greater quantity, together with an excess of uric acid, after meals, and therefore to be related to the production of the latter in the body; but it probably is chiefly derived from oxalates being contained in some materials taken with the food.

Colouring Matters.

It appears probable that the colour of the urine depends on the presence of small quantities of distinct substances which have different origins in the body. Three such have been described, and may be taken provisionally to represent our knowledge of the subject :—

1. *Urobilin*, which is an outcome of the colouring matter of the bile, and therefore a remote derivative of the colouring matter of the blood, is frequently present in the urine. It is probably the same as hydrobilirubin, some of which is occasionally absorbed from the intestinal tract and eliminated by the kidneys.

2. *Urochrom* is said to be the special pigment of the urine. It oxidises on exposure, forming a reddish substance that gives the dark colour to some urinary sediments (*Uroerythrin*).

3. A certain material (*Indican*) capable of producing *Indigo*, is commonly present in the urine of man, and in greater quantity in that of some animals, particularly the horse. It is supposed to be formed from the indol that arises from the putrefactive changes consequent on the pancreatic digestion. The indol is absorbed and unites with sulphuric acid to form Indican, which is a yellow substance. Under certain conditions it can be converted by oxidation into indigo-blue.

Inorganic Salts.

The urine is the great outlet for all inorganic salts. The most important of these are—

Common salt (NaCl.) of which a very variable, but always considerable amount passes away in the urine. The average quantity excreted per diem may be said to be about half an oz. (15 grammes). It depends greatly on the quantity taken with the food, and falls during starvation, but does not completely disappear. It is said that if absolutely no common salt be taken with the food the quantity of NaCl. excreted diminishes greatly, and albumin appears in the urine about the third day. The amount of salt eliminated follows, with striking accuracy, the changes that take place at different times and

under different circumstances, in the quantity of urea excreted. These facts seem to indicate that there is some relationship between the secretion of the two bodies, or that sodium chloride participates in the chemical changes of the nitrogenous tissues. In many diseases there occur variations in the quantity of common salt in the urine which can hardly be explained by the change in, or absence of food.

Phosphates.—About 60 grains (3 to 4 grammes) of phosphoric acid is excreted daily in the urine, being combined with alkalies to form salts, viz., potassium, sodium, calcium, and magnesium phosphates.

Sulphates.—Nearly 40 grains (2 to 3 grammes) of sulphuric acid, as sulphates of alkalies, are daily got rid of in the urine. The acid comes partly from the food, but chiefly from the oxidation of the sulphur contained in the proteids of the tissues.

A considerable quantity of *potassium*, *sodium*, *calcium*, and *magnesium*, combined as already mentioned, or with chlorine, is contained in the urine.

Small traces of *iron* are also always present in the urine.

Gases.—The urine also contains free CO_2, N, and some O. 100 volumes of gas pumped out of fresh urine have been found to consist of—

$CO_2 = 65{\cdot}40$ per cent.
N $= 31{\cdot}86$ „
O $= 2{\cdot}74$ „

Abnormal Constituents.

Different kinds of substances occur in urine under circumstances of special physiological interest, and therefore may be here enumerated, although their accurate study belongs rather to pathology. First amongst these to be named is,—

Albumin, which occurs from (1) any great increase in the blood-pressure in the renal vessels, whether caused by increased inflow or impeded outflow. (2) Excess of albumin in the blood, and, strange to say, some forms of albumin escape much more readily than others. Thus, egg albumin, globulin, or peptone, if introduced artificially into the blood, are soon found in the urine. (3) A watery condition of the blood, such as would give rise to œdema elsewhere. (4) Total abstinence from NaCl. for some time. (5) Destruction of some of the epithelium of the urinary tubes.

Next in importance to albumin are the following :—

Grape sugar; of which normally only the merest trace occurs in

the urine, although there is always a certain quantity in the blood. It is present in large quantities in (1) the disease known as diabetes, when a great quantity of pale urine with a very high specific gravity is passed. (2) After injury of a certain part of the floor of the 4th ventricle of the brain. (3) After poisoning by curara, carbonic oxide, and nitrate of amyl. In short any disturbance of the circulation of the liver gives rise to an increase of sugar in the blood, and when the amount reaches 6 per cent. it appears in the urine.

Bile Acids and *Pigments* appear in the urine when, from occlusion of the bile ducts, they find their way into the blood.

Leucin and *Tyrosin* also occur in the urine, but only after interference with the function of the liver.

The urine undergoes important changes after being voided, the explanation of which is of much interest to the practitioner, and must be understood by the student of medicine. The urine often loses its transparency as soon as it gets cold, though perfectly clear when passed, or when again heated to the body-temperature, for the urates are soluble in warm but almost insoluble in cold water. This "muddiness," which soon settles down, as a more or less brightly coloured sediment, is chiefly caused by the precipitation of acid sodium urate, stained with a colouring matter derived from the urochrome. When this occurs the urine will always be found to be distinctly acid, and if it be left standing for some time in a cool place, the acidity will be found to increase, owing to the presence of a peculiar fungus which sets up *acid fermentation*. This is said to depend on the formation of lactic and acetic acids, and crystals of uric acid, amorphous sodium urate, and crystals of lime oxalate are deposited.

After a certain time (which is shorter when the urine is not very acid and is exposed to a warm atmosphere) the development of bacteria occurs in it, and causes the urea to unite with water, and to change in the manner already mentioned (p. 46) into ammonium carbonate. This gradually neutralises the acidity, and finally renders the urine alkaline. At the same time an amorphous precipitate of lime phosphate appears, and crystals of ammonio-magnesium phosphate and of ammonium urate are produced.

Urinary Calculi.

Various ingredients of the urine, which are difficult of solution, sometimes become massed together as concretions, particularly if there exist any small foreign body in the bladder, which, by acting

as a nucleus, lays the foundation of a stone. Sometimes small concretions are formed in the tubes or pelvic recesses of the kidney, and, when these make their way into the bladder, they commonly grow larger and larger. The structure and composition of a calculus often gives the history of its own transit from the kidney, and also of various changes in the metabolism of the individual, for successive layers of different substances are generally found in a stone that has attained any great size. The chief materials found in calculi are—uric acid, ammonium urate, calcium oxalate and carbonate, ammonio-magnesium phosphate, &c.

Source of Urea, &c.

The question as to whether the chief materials of the urine pre-exist in the blood and are therefore merely removed by the kidney, or are manufactured by the special powers of the renal cells, has been widely discussed, and though the great weight of evidence is in favour of the former view, some of the experimental results on the subject are rather conflicting.

The following are the more important points in the argument:—

1. The blood normally contains most of the important substances found in the urine; so they need not necessarily be made in the kidney.

2. The blood in the vessel leading to the kidney—the renal artery—is said to contain more urea than the vessel leading from it—the renal vein—so that the blood appears to lose urea in passing through the kidney.

3. If the ureters be tied and the elimination be thus prevented, urea accumulates in the blood. This can hardly be made by the kidney, because—

4. If the renal arteries be tied so that no blood goes to the kidneys to effect the elaboration of urea in those organs, then the same accumulation results, showing that the kidneys are certainly not the only organs where urea is made.

5. Extirpation of the kidneys also gives rise to a great increase of the urea in the blood. The amount of urea in the blood after nephrotomy is said to increase steadily with the time which elapses after the operation, and the amount accumulated corresponds to the amount that would normally have been excreted in the same time, had the animal not been operated upon.

6. In some diseases which interfere with, or suppress the secretion of the kidneys, an accumulation in the blood of certain poisonous

or injurious materials takes place, and gives rise to the gravest symptoms called uræmic poisoning, which closely coincide with those observed in experimental annihilation of the renal function.

From the foregoing it would appear to be satisfactorily settled that the urea, which is by far the most important ingredient of the secretion of the kidney, is probably made elsewhere and not in that organ, whose duty seems to be chiefly to remove it from the blood. This is most probably also true of all the other organic constituents of the urine. The question then arises, where is the urea formed ?

We naturally turn for an answer to the most wide-spread and most actively changing nitrogenous tissue, namely muscle. Here we find only a partial explanation of the source of urea, for neither does muscle contain much urea, nor does active muscular work perceptibly increase the general urea elimination. In muscle, however, a material closely allied to and readily convertible into urea, namely kreatin, occurs, and it has been suggested that this substance is changed into urea in the kidney. This cannot explain the origin of all the urea, for, as already remarked, the amount of urea excreted does not correspond with the muscle metabolism.

A considerable quantity of urea no doubt comes from muscle, which tissue forms so large a part of our bodies, but we must conclude that there are many other sources of urea, because there are many other organs where nitrogenous substances are undergoing chemical changes and gradual waste.

The liver is specially worthy of note as a source of urea, since it helps to explain the striking relation between the amount of albuminous food and the quantity of urea eliminated. There can be no doubt that most people consume much more albuminous food than is necessary for the adequate nutrition and preservation of the nitrogenous tissues, and therefore must have a surplus of nitrogenous material. It may be remembered, as was pointed out in the chapter on Digestion, that in all parts of the alimentary tract there is a limit to the absorption of peptones, and that in the small intestine when delay in absorption occurs the decomposition of peptones results, because in prolonged pancreatic digestion these peptones are changed into leucin ($C_6H_{13}NO_2$) and tyrosin ($C_9H_{11}NO_3$) and as such pass into the portal circulation to be borne to the liver. In the liver it is highly probable that these bodies are converted into urea, for, when they are introduced into the intestinal tract, they are absorbed and an excess of urea appears in the urine. Thus the surplus of the proteid food, before it really enters the system, is broken up in the intestine into bodies which, notwithstanding the difficulty of explain-

ing the chemical process, may be regarded as a step towards the formation of urea. This view is supported by the facts that (1) in disease of the liver tyrosin and leucin appear in the urine; (2) if these bodies be introduced into the general circulation, by the jugular instead of the portal vein, they are excreted unchanged by the kidneys.

Nervous Mechanism of the Urinary Secretion.

With regard to the influence exerted by the nervous system on the renal secretion, we have but little satisfactory information, although there can be no doubt that here, as in other glands, the process is under the control of the nerves. Many of the circumstances which cause greater activity of secretion, such as taking large quantities of water, &c., have no effect on the general blood pressure, so that, if the increased flow be brought about by the vaso-motor mechanisms, it must be by means of nervous channels altering the blood flow in the special arteries of the glands. Further, some emotional conditions exist, such as hysteria, in which an unaccountably great quantity of urine of very low specific gravity is evacuated.

With regard to the effects of the vaso-motor nerves, we know that section of all the nervous twigs going to the kidneys causes great congestion and an immense increase in the secretion, which commonly contains albumin. This no doubt depends on the sudden rise in pressure in the glomeruli, owing to the dilatation of the arterioles. If the splanchnics, in which the renal vaso-motor nerves run, be cut, a great quantity of urine is produced from the same cause—vaso-motor paralysis—but, on account of the large area of vessels injured, the general blood pressure falls, and therefore the effect is not so much marked. If the peripheral end of the cut nerves be stimulated, the secretion is diminished, and, owing to spasm of the renal arterioles and fall of blood pressure in the glomerular capillaries, may be brought to a standstill. Section of the spinal cord at the 7th cervical vertebra stops the flow, because it so reduces the general blood pressure that the pressure in the renal vessels falls below that necessary for the filtration of the urine.

The introduction of various substances into the blood causes a marked change in the blood supply of the kidney and the amount of urine secreted. These changes do not correspond with the changes in general blood pressure occurring during the experiments.

Passage of the Urine to the Bladder.

The pressure exerted by the blood in the glomerular capillaries is quite sufficient to make the urine flow from the pelvis of the kidneys into the bladder, because when the ureters are tied they become distended above the ligature by the urine flowing from the pelvis, where a pressure may be produced of some forty millimetres of Hg., at which pressure the secretion stops and becomes somewhat changed in chemical composition (kreatin appearing in greater quantity).

Normally, however, the passage of the urine along the ureters is accomplished by the peristaltic motion of the ducts, which goes on alternately in the two ureters, so that the urine flows into the bladder at different periods from the right and left kidney.

The ureters have a strong middle coat of encircling fibres of smooth muscle along which a wave of contraction, lasting about one-third of a second, passes rhythmically in about 6 to 10 seconds from the pelvis of the kidney to the bladder.

Having reached the bladder, the urine cannot return into the ureters on account of the oblique way in which these ducts pass through the walls of the bladder. When the pressure in the bladder increases, the opening of the ducts becomes closed and acts as a kind of valve.

Retention of Urine in the Bladder.

The urine, which is continuously secreted and rhythmically conveyed to the bladder, is only voided at convenient times ; therefore special arrangements exist for its retention and expulsion.

The *retention* of urine in the bladder up to a certain point depends on the elasticity of the parts concerned, the dense elastic tissues around its outlet being able to resist the elastic force exerted upon its contents by the walls of the bladder and the viscera. Thus where no active muscular forces can possibly come into play, as in the case of the dead subject, or in complete paralysis following destruction of the spinal cord, a considerable amount of urine is retained. But when a certain pressure is arrived at by the gradual accumulation of urine within the bladder, the elasticity of the sphincter and the other tissues around the outlet is overcome by the elasticity of the bladder wall, and the urine slowly dribbles away.

In the normal condition, however, the urine is retained by a muscular mechanism over which we have acquired considerable voluntary control.

This is the *sphincter* muscle, which, by contracting, helps the elastic power of the tissues around the urethra and retains the urine. The accumulation of urine after a certain time gives the sensation known as a full bladder, but this feeling is not necessarily accompanied by any irresistible call to make water, though it soon produces a desire in that direction. We suppose that the stimulus given to the afferent nerves by filling the bladder reflexly causes a constriction of the spincter muscle, so that, in proportion as the pressure within the bladder increases, the resistance to its outflow is also augmented. This does not imply any automatic action of the sphincter vesicæ, but merely a constant reflex excitation of that muscle, which secures its contraction and the retention of a considerable amount of urine without the intervention of voluntary influences or attention. When the bladder becomes very full the reflex mechanism may require the assistance of the voluntary centres to augment this power and prevent the urine being evacuated.

Evacuation of the Bladder.

Micturition, or the expulsion of the urine, does not normally depend on elastic forces alone, as in the case mentioned of paralytic incontinence, when the urine commences to dribble away as soon as a certain pressure is attained within the bladder, but is accomplished by the *detrusor urinæ* muscle which lies in the wall of the bladder.

Under ordinary circumstances there is a relationship between the expelling and retaining powers (neither the muscle in the wall of the bladder nor voluntary effort, however, coming into action), in which the retaining power of the sphincter is just able to resist the elastic pressure. If the urine be retained for a considerable time the reflex stimulation of the sphincter no longer suffices to keep back the fluid, and the voluntary effort has to be called to the aid of the reflex action of the sphincter. If a drop of urine happen now to make its way into the sensitive urethra matters are altered. Even voluntary effort does not suffice to keep back the stream, and an irresistible call to empty the bladder is made upon the spinal nerve mechanisms. This is accomplished by the contraction of the muscular coat of the bladder which is excited reflexly by the stimulus starting from the mucous membrane lining the urethra.

When the urine once commences to flow it continues until the bladder is quite empty, the last drops of urine being expelled from the urethra by rhythmical spasms of the muscles around the bulbous portion of that canal. The sequence of events will then be,—(1)

stimulation of the mucous membrane of the urethra by a drop of urine ; (2) contraction of the detrusor urinæ ; (3) relaxation of the sphincter ; (4) rhythmical contraction of the ejaculator urinæ, and, finally, a twitch of the levator ani and neighbouring muscles.

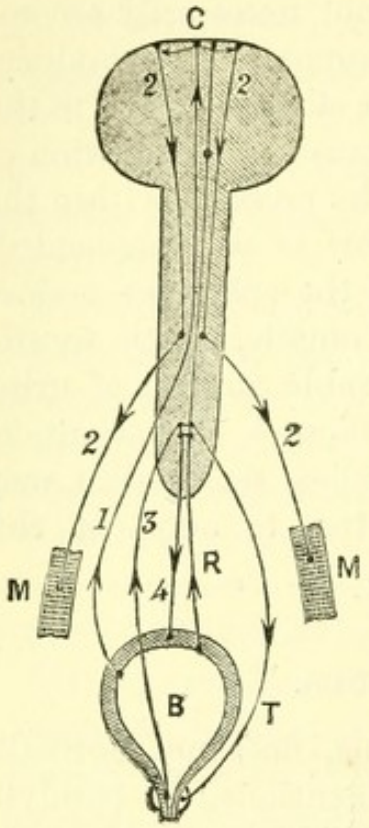


Fig. 176.—Diagram of the Nervous Mechanism of Micturition.

B. Bladder.

M. Abdominal muscles.

C. Cerebral centres.

R. Represents impulses which pass from the bladder to the centre in the spinal cord, whence tonic impulses are reflected and pass along T to sphincter, which retains the urine.

When the bladder is distended, impulses pass to the brain by 1, and when we *will*, the tonus of the spinal centre stimulating the sphincter is checked, and the abdominal muscles are made by 2 to force some urine into neck of bladder, whence impulses pass by 3 to inhibit the sphincter centre and excite the detrusor through 4.

The evacuation of the bladder is under these circumstances accomplished independently of the will by a reflex act, of which we may even be unconscious.

This reflex micturition may occur during the sleep, as the result of slight local excitations. In infants this is the normal mode of emptying the bladder, and the gradual education of the centres controlling the retention mechanisms is watched with interest in young children.

At an early age, generally, we learn to control the acts of these centres by our will. We feel a desire to empty the bladder before it become so distended that the reflex contraction of the sphincter is insufficient to retain the urine. But the volition serves to call into activity the reflex mechanism just described. Almost at any time we can call forth the reflex act by increasing the pressure on the bladder by voluntary contraction of the abdominal muscles ; the diaphragm being depressed and fixed, the muscles of expiration are put into action so as to press upon the pelvic viscera. At the same time the contraction of the sphincter muscle is probably checked by the will, and thus the power of retention is overcome.

The moment the balance of power is thus turned in favour of the expelling agencies a drop of urine reaches the beginning of the urethra and excites reflexly the spinal centres, and thus brings about the complete evacuation of the bladder without further voluntary effort.

The *nervous mechanism* that controls the act of micturition consists essentially of ganglionic centres which are situated in the lumbar enlargement of the spinal cord, and of two sets of nerve channels passing to and from these centres. The centres may be said to be composed of functionally distinct parts—a *retaining* and *evacuating* part. The retaining centre causes the sphincter muscle to contract. The evacuating centre can excite the detrusor to action. One set of nerve channels (3, 4, R, T) communicates between these centres and the urinary organs (B), and the other (1, 2) between the cord centres and the cerebral hemispheres (C). That which connects the special *lumbar centres* with the bladder, contains *efferent* fibres of two kinds, going to the antagonistic muscles, the sphincter vesicæ (T), and the detrusor urinæ (4) respectively, and *afferent* fibres of different kinds ; those (R) going from the bladder to the nerve cells in the cord which stimulate them and cause the sphincter to remain tonically contracted, those passing from the mucous membrane of the urinary passages to the ganglionic cells in the cord have two functions ; one (4) excites the contractions of the detrusor urinæ and the other (3) inhibits the tonic action of the retaining centre.

The action of the ganglionic cells that stimulate the sphincter muscle can to a certain extent be either aided or checked by means of voluntary or other cerebral influences, so that two kinds of fibres —a stimulating and inhibitory one—must pass from the hemispheres to the micturating centre in the cord.

Those cells which govern the motions of the detrusor seem to be least under voluntary control, and are probably only stimulated to action by the impulses arising from the urinary passages, and hence are simply reflex centres.

The effect of certain emotions on the act of micturition seems to show that those ganglion cells in the cord which cause the bladder to contract are connected with the higher centres. Thus, extreme terror (in a dog at least) often causes a forcible expulsion of urine, and great anxiety or impatience seems in man often to have a checking influence, causing great delay in initiating micturition.

CHAPTER XXIII.

NUTRITION.

We can compare the incomings and outgoings of the economy, and should now be in a position to see what light can be thrown by this comparison upon the actual changes which take place in the textures of the body.

We have seen that the income is made up of substances belonging to the same groups of materials as are found in the body, viz., albumins, fats, carbo-hydrates, salts, and water, introduced by the alimentary canal, and oxygen, which is acquired by the respiratory apparatus; whilst the outgoings consist of urea from the kidneys, carbonic acid from the lungs, certain excrement from the intestine and other mucous passages, sweat, sebaceous secretion, epidermal scales, from the skin; together with a quantity of water from all these ways of exit. The milk, ova, and semen, may be here omitted, being regarded as exceptional losses devoted to special objects.

In order that the body may be kept in its normal condition, it is necessary that the income should at least be equal to the outgoings of all kinds, and, except where growth is going on rapidly, an income equal to the expenditure ought not only to suffice, but ought to be the most satisfactory for the economy.

We know that animals can live for some considerable time without food, in which case a certain expenditure of material derived from the body itself is necessary to sustain life, and therefore the outgoings continue. We ought thus to be able to arrive in a very simple manner at the minimal expenditure necessary for the sustentation of the body. We shall find, however, that (1) an income equal to this minimal expenditure (that of starvation) does not at all suffice to keep up the body-weight, and that (2) a considerable margin over and above this minimum is necessary in order to establish the nutritive equilibrium; (3) further, that the proportion of material eliminated and stored up in the body respectively varies

as the income is increased; (4) and finally, that the quality of the food—*i.e.*, the proportion of each group of food-stuff present in the diet—has an important influence on the quantity required to establish the equilibrium, and that best suited to cause increase of weight or to fatten.

It will be convenient to consider the following different cases in succession.

1. No income, except oxygen, *i.e.*, starvation.
2. An income only equal to the expenditure found during starvation.
3. Establishment of perfect nutritive equilibrium.
4. Excessive consumption.

Tissue Changes in Starvation.

As is well known, deprivation of oxygen—by cessation of the respiratory function—almost immediately puts an end to the tissue-changes necessary for life, so that the oxygen-income cannot be interfered with or the experiment comes to an end. It has also been found that a small supply of water to drink makes the investigation of the various tissue-changes more reliable, by facilitating them and prolonging life. We therefore speak of a total abstinence from solids as starvation.

When deprived of food, those tissues upon the activity of which life immediately depends must feed upon materials stored up in some tissues of less vital importance to the animal. The first questions to discuss are how much the body loses daily in weight during the time that it is thus feeding on itself, and how far the different individual tissues contribute to this loss.

The general loss of weight is directly estimated by weighing the animal, and the loss of the individual tissues is calculated by a careful analysis of the various excreta, by which the exact amount of nitrogen, carbonic acid, &c., is ascertained: the nitrogen corresponds to the loss of muscle; and the carbon (after excluding that portion which is the outcome of muscle change, which may be calculated from the nitrogen) corresponds to the fats oxidised.

Loss of weight.—It has been found that a starving animal loses weight rapidly at first, and subsequently more slowly. The cause of this difference is that the food last eaten continues to have influence during the first three or four days, and the materials eliminated are proportionately large in quantity. When the influence of the food

taken prior to starvation has ceased, the daily amount of materials eliminated is much reduced and remains nearly constant, decreasing slightly in proportion as the body-weight diminishes slowly until the animal's death.

Adult animals generally live until they have lost about half of their normal body-weight. Young animals die when they have lost about 20 per cent. of their weight.

Relative loss in various tissues.—Roughly speaking, we may take the body of a man to be made up of the following proportions of the more important textures :—

Muscles	50 per cent.
Skin and fat	25 ,,
Viscera	12 ,,
Skeleton	13 ,,

Seeing that the muscle tissue contributes such a large proportion to the body-weight, we cannot be surprised that in starvation the greatest *absolute loss* occurs in this tissue ; except in the case of excessively fat animals. Next comes adipose tissue, which almost entirely disappears, so that the *relative loss* is here greatest, but the absolute loss varies in proportion to the fatness of the animal at the beginning of the investigation. The spleen and liver lose more than half their weight, and the amount of blood is greatly reduced. The smallness of the loss that occurs in the great nervous centres is very striking. They seem to feed on the other tissues.

The following table gives the approximate *per centage* of loss which takes place in each individual tissue during starvation :—

Fat	97·0 per cent.
Muscle	30·2 ,,
Liver	56·6 ,,
Spleen	63·1 ,,
Blood	17·6 ,,
Nerve-centres	0· ,,

With regard to the *portals by which the various materials make their escape*, it has been found that practically all the nitrogen passes off with the urine, and about nine-tenths of the carbon escapes by the lungs as CO_2, the remaining one-tenth passing off by the intestine and kidneys. Three-fourths of the water is found in the urine, and one-fourth goes off from the skin and lungs.

The following table shows the items of the general loss, and the amount per cent. which passes out by the chief channels of exit :—

	Total Elimination.	Via Kidneys.	Lungs and Skin.	Excrement.
Water . .	995·34 grm.	70·2 %	26·1 %	3·7 %
Carbon . .	205·96 „	6·4 %	92·6 %	1·9 %
Nitrogen .	30·81 „	100·0 %	—	—
Salts . .	10·03 „	97·0 %	—	2·4 %

As the loss of weight of an animal's body during starvation is at first rapid and then more gradual, so also the amount of material eliminated is found to diminish much more slowly after the first few days. This is well seen from the nitrogenous elimination. For the first four days the fall in the amount of urea excreted is very rapid, it then decreases slowly and almost constantly until the death of the animal. The subsequent fall is in proportion to the slow decrease in weight of the animal. This has led to the conclusion that the nitrogenous material eliminated during a full diet comes partly from used-up nitrogenous tissues, and partly from nitrogenous materials which have never really entered into the composition of the tissues, but are the surplus of nitrogenous food. Hence, two kinds of proteid are supposed to exist in the body, viz., (1) that forming part of the tissues, and (2) that circulating as a ready supply for the nutritive demands of the tissues.

An Income Equal to the output of Starvation.

In the second case mentioned, namely, where an amount of food is supplied which is just equal to the expenditure which was found to take place during starvation, one might suppose that the diet, though minimal, would yet suffice to preserve the normal body-weight. Practice, however, shows this to be far from being the case.

An animal fed on diet equal in quantity to the outgoings during starvation continues to lose weight, and the quantity of nitrogenous substance eliminated (urea) is in excess of the low standard found during complete abstinence from food. From this it would appear that even when supplied with an amount of nitrogenous material equal to that used by the tissues during starvation, an animal takes a further supply from its own textures, and eliminates some of the nitrogenous nutriment without using it. The body

subsists on the scanty allowance of nutriment it borrows from the tissues during starvation, only so long as there is absolutely no food income, when food is supplied an increased expenditure is set up, the income is exceeded, and a deficit occurs in the nitrogen balance. Or probably some of the nitrogenous nutriment is rendered useless by the processes it undergoes in the intestine, even when the quantity is not sufficient to support the equilibrium (compare pp. 127, 346).

It follows, then, that feeding an animal on an amount of food-stuffs exactly corresponding to the quantity of nutriment abstracted from its own textures during total abstinence is only a slower form of starvation.

With regard to nitrogenous substances, it has been proved that nearly three times as much as the amount eliminated during starvation is required to establish an equilibrium between the income and expenditure of those special substances, and that less than this leads to a distinct nitrogenous deficit.

Nutritive Equilibrium.

The third case mentioned, viz., that in which the nutritive equilibrium is exactly maintained, so that the body-weight remains unaltered, is the most important one for us to determine, since its final settlement would enable us to fix the most beneficial standard of diet. Unfortunately, this case is also the most difficult upon which to come to a satisfactory conclusion, for the following reasons :

1. The elaborate nature of the conditions imposed during the experiment makes it difficult to carry on the investigation with scientific accuracy.

2. Even when the amounts of gain and loss exactly correspond we cannot say that we have the best dietary ; because some of the income may be quite useless, and pass through the economy without performing any function, and yet appear in the output so as to give an accurate balance.

3. We have just seen that the relative amounts of outgoings and of material laid by as store are altered and regulated by the *quantity* of income. And we find that the *quality* of the income, *i.e.*, the relative proportions of the various food-stuffs, has a material influence on the quantities of material laid by and eliminated respectively. We must, therefore, consider the efficacy of each of the groups of the food-stuffs when employed alone and mixed in different proportions.

4. Different animals seem to have different powers of assimilation; and under various circumstances the requirements and assimilative power of the same animal may vary.

Nitrogenous diet.—An animal fed upon a purely meat diet requires a great amount of it to sustain its body-weight. It has been found that from $\frac{1}{20}$ to $\frac{1}{25}$ of the body-weight in lean meat daily is necessary to keep an animal alive without either losing or gaining weight. If more than this amount be supplied the animal increases in weight, and as its weight increases a greater amount of meat is required to keep it up to the new standard. So that to produce a progressive increase of weight with a purely meat diet, it is necessary to keep on increasing the quantity of meat given. The reason of this is found in the fact that albuminous diet causes an increase in the changes occurring in the nitrogenous tissues.

If an animal which is in extremely poor condition be given an *ad libitum* supply of lean meat, only a limited portion of the albuminous substance is retained in the tissues. By far the larger proportion of the nitrogenous food is given off and is represented in the urine by urea, and a comparatively small proportion is stored up. If this large supply of meat diet be continued for some time, less and less of the albuminous material is stored, more and more being eliminated as urea, until finally the urea excreted just corresponds to the albuminous materials in the ingesta. When only meat is given, it must be supplied in large quantities to maintain the balance of nitrogenous income and expenditure which is spoken of as nitrogenous equilibrium. Upon the occurrence of a change in the amount of nitrogenous ingesta, this nitrogenous equilibrium varies, and it takes some time to become re-established, because a decrease in the meat diet is accompanied by a decrease in the weight of the animal, and an increase causes it to put on flesh. For each new body-weight there is a new nitrogenous equilibrium, which is only attained after the disturbed relation between the nitrogenous ingesta and excreta has been re-adjusted.

The increase of weight which follows a liberal meat diet depends in a great measure on fat being stored up in the body. Much more of this material is made than could come from the fat taken with the meat; hence, we must conclude that it is made from the albuminous parts of the meat.

Non-nitrogenous diet.—The effect of a diet without any albuminous food is that the animal dies of starvation nearly as soon as if deprived of all forms of food, with the exception that the weight of the body is much less reduced at the time of death.

Mixed diet.—The addition of fat or sugar to meat diet allows of a considerable reduction in the supply of meat, both the body-weight and nitrogenous tissue-change preserving their equilibrium on a smaller amount of food. It has been estimated that the nitrogenous tissue change is reduced 7 per cent. by the addition of fat, and 10 per cent. by the addition of carbohydrate food to the meat diet; therefore less meat is wanted to make up nitrogenous tissues. Further, fats and sugars, which obviously cannot of themselves form an adequate diet, since they contain no nitrogen, seem to have the power of accomplishing some end in the economy which, in their absence, requires a considerable expenditure of nitrogenous materials to bring about. Fats and sugars, then, supply to the body readily oxidisable materials, and thus shield the albuminous tissues from oxidation, as well as reduce absolutely the nitrogenous metabolism.

It would further appear from the experience gained from the stall-feeding of animals that a good supply of carbohydrates, together with a limited quantity of nitrogenous food, is admirably adapted to produce fat. Since much more fat has been found to be produced in pigs than could be accounted for by the albuminous and fatty constituents of their diet, we must suppose that from their carbohydrate food fat can be manufactured in their body.

Much of the difficulty found in reconciling the opinions of different authors concerning the sources of fat in the body can be removed, and some knowledge of the manufacture of fats from the food-stuffs can be gained by bearing in mind the properties of the protoplasm. There can be no doubt that protoplasm if properly nourished can manufacture fat. As examples, we may take the cells of the mammary gland and connective tissue. This fat production may be regarded as a *secretion* of fat, though only in one of the examples given does it appear externally as a definite secretion—milk. We cannot scrutinise the chemical methods by which this change is brought about in protoplasm, any more than those which give rise to the special constituents of other secretions. We know that protoplasm uses as pabulum, albumin, fat, and carbohydrate, and we have no reason to doubt that the proportion of these materials found to form the most nutritious diet for the body generally, is also the proportion in which protoplasm can best make use of them. Probably cells which secrete a material containing nitrogen, such as mucin-yielding gland-cells, require a greater proportion of albumin. Those cells which produce a large quantity of non-nitrogenous material may not require more nitrogen than is necessary for their perfect re-integration as nitrogenous bodies. In the manufacture of their secretion, they

only require a pabulum which contains the same chemical elements as are to be found in the output. In the case of fat-formation a supply of fat or carbohydrate ought to suffice if accompanied by a small amount of albuminous substance. If these non-nitrogenous substances be withheld, the protoplasm could no doubt obtain the quantity of carbon, hydrogen, and oxygen requisite to manufacture fat from albumin, but this would not be economical, for a large amount of nitrogen would be wasted.

Fat cannot be produced by the tissue cells without nitrogen in the diet, because the fat-manufacturing protoplasm cannot live without nitrogen, which is absolutely necessary for its own assimilative re-integration. A good supply of nitrogenous food aids in fattening, since it gives vigour to all the protoplasmic metabolism, and among them fat-formation.

The albuminoid substance *gelatine*, which is an important item in the food we ordinarily make use of, is able to effect a saving in the albuminous food-stuffs. Although it contains a sufficiently large proportion of nitrogen, it cannot satisfactorily replace albumin in the food. Indeed, in spite of the great similarity in its chemical composition to albuminous bodies, it can no better replace the proteids in a dietary than fat or carbohydrate; and, although an animal uses up less of its tissue nitrogen on a diet containing gelatine and fat than when it is fed on fat alone, it dies of starvation almost as if its diet contained no nitrogenous substance.

Excessive Consumption.

The last case we have to consider is that in which the supply of food-material is in excess of the requirements of the economy. This is certainly the commonest case in man.

Much of the surplus food never really enters the system but is conveyed away with the fæces.

In speaking of pancreatic digestion, reference has been made to the possible destiny of excess of nitrogenous food. In the intestine, some of it is decomposed into leucin and tyrosin, which are absorbed into the intestinal blood-vessels. In the body these substances undergo further changes, which probably take place in the liver. As a result of the absorption of leucin, a larger quantity of urea appears in the urine, and hence the leucin formed in the intestine by prolonged pancreatic digestion, is an important source of urea. This view is supported by the almost immediate increase

in the quantity of urea eliminated when albuminous food is taken in large quantity.

From the fact that a considerable amount of fat may be stored up by an animal supplied with a liberal diet of lean meat, we must conclude that part at least of the surplus albumin goes to form fat. It has been suggested that after sufficient albumin has been absorbed for the nutritive requirements of the nitrogenous tissues, the rest is split up into two parts, one of which is immediately prepared for elimination as urea by the liver, and the other undergoes changes, probably in the same organ, which result in its being converted into fat.

It would further seem probable, from the manner in which the urea excretion changes during starvation, that, as before mentioned, the absorbed albumin exists in the economy in two forms: one in which it has been actually assimilated by the nitrogenous tissues and forms part of them, and hence is called organ-albumin; the other, which is merely in solution in the fluids of the body, being in stock, but not yet ultimately assimilated, and hence called circulating albumin. The latter passes away during the first few days of starvation, being probably broken up to form urea, and a material which serves the turn of non-nitrogenous food. The organ-albumin appears to supply the urea after the circulating albumin has completely disappeared.

From the foregoing it will be gathered that we cannot say what are the exact destinies of the various food-stuffs in the body. Proteids are not exclusively utilised in the re-integration of proteid tissues, as an excess gives rise to a deposit of fat. Carbohydrates are not employed simply to replace the carbohydrates constituting part of the tissues, but as will be shown when speaking of muscle metabolism, they are intimately related to the chemical changes which take place during the activity of that tissue. If fats are chiefly devoted to the restitution of the fat of the body, they certainly are not the only kind of food from which fat can be made.

We may say, then, that all food-stuffs are destined to feed the living protoplasm, whether it be in the form of gland cells, the cells of the connective tissues, or muscle-plasma, so that all the food-stuffs that are really assimilated contribute to the maintenance of protoplasm and subserve to its various functions. Besides nourishing itself and keeping itself up to a certain standard composition, protoplasm, or rather the various protoplasmata, can make the various chemical materials we find in the body. Some produce fat, some animal starch (glycogen), and others manufacture the various substances we find in

the secretions ; while yet another group is devoted to setting free and utilising the energy of the various chemical associations.

But all the food we eat is not assimilated ; indeed, the destiny of the numerous ingredients of our complex dietaries is not easily traced. Of food-stuffs proper the following classification may be made, showing that even the same stuff may meet with a different fate under different circumstances—

1. Stuffs which never enter the economy (fæces).
2. Materials absorbed and arriving at the blood are at once carried to certain portals of excretion (excess of salts).
3. Substances which are broken up in the intestine to facilitate their elimination (excess of proteid).
4. Substances absorbed and carried along by the fluids, but not really united to the tissues (circulating albumin).
5. Materials which after their absorption are really assimilated by the protoplasm of the tissues (a certain amount of all food-stuffs).
6. Substances which, after their assimilation by the protoplasm, reappear in their original form, and are stored up (fats).

The question of the exact amounts and materials required to form the most economic and wholesome dietary is one of too great practical importance to receive adequate attention in this manual. As a rule men, like other animals, partake of food largely in excess of their physiological requirements when they can get it. This may be seen by contrasting one's own daily food with the amount which has been found to be adequate in the case of individuals who have not the opportunity of regulating their own supplies of comestibles.

An adult man should be well nourished if he be supplied with the following daily diet :—

Albuminous foods .	100 grms.	or	3·5 ozs.
Fats	90 „	„	3·1 „
Starch . . .	300 „	„	10·7 „
Salts	30 „	„	1·0 „
Water	2000 „	„	3 pints.

As a matter of fact, many persons do thrive on a much less quantity of proteid than that given in this table, but in their case the fats and starches should be proportionately increased.

Such a dietary could be obtained from many comestibles alone, and hence the taste of the individual may be exercised in selecting his

food without much departing from such a standard. Individual taste commonly selects foods with too much proteid—*i.e.*, an excess of nitrogen—whilst the cheapness of vegetable products dictates their use in greater abundance as food.

Compare Chap. V., p. 69, where the quantity of the different food-stuffs in some of our common articles of diet is given.

CHAPTER XXIV.

ANIMAL HEAT.

THE bodies of most animals are considerably warmer than their surroundings. Part of the energy set free by the chemical changes in the animal tissues appears as heat which is devoted to this purpose. *Warm-blooded* animals are those which habitually preserve an even temperature independent of the changes which take place in that of the medium in which they live; and, as the term warm-blooded implies, their temperature is as a rule higher than the surrounding air or water. *Cold-blooded* animals, on the other hand, are those whose temperature is considerably affected by, or more or less closely follows, that of the medium surrounding them.

The blood of all mammalia has pretty much the same temperature as that of man, about 37·5° C., and probably varies under similar circumstances. But birds, the other class of warm-blooded animals, have a temperature about 4° or 6° C. higher than that of mammals.

The blood of those animals whose temperature follows the changes that occur around them, is generally from 1° to 5° C. higher than the medium in which they live. They produce some heat, though it be small in quantity, and since they have no special plan for its regulation, it does not remain at a fixed standard. In every part where active oxidation takes place, heat is produced; so even in invertebrate animals an elevation of temperature occurs; this can be ascertained where they exist in masses, as in bee-hives, an active hive sometimes reaching a temperature of 35° C.

Instead of the term "warm-blooded," it is more accurate to apply to animals whose temperature remains uniformly even, and independent of their surroundings, the term "*Homœothermic*" (of constant temperature), and to animals with temperatures varying with their surroundings "*Poikilothermic*" (of changing temperature), instead of the words warm- and cold-blooded.

Measurement of Temperature.

On account of the slight amount of variation that occurs in the temperature of man, all the changes can be measured with a thermometer having a short scale of some 20 degrees, each degree of which occupies considerable length on the instrument, so that very slight variations may be easily appreciated. Such thermometers, with an arrangement for self-registering the maximum height attained by the column of mercury, are in daily use for *clinical* observation, for the temperature of the body is now a most important aid to diagnosis and prognosis in a large class of diseases.

As heat is constantly being lost at the surface of the body, the skin is colder than the deeper parts, and in order to avoid variations caused by this surface loss—which depends in a measure on the temperature of the air—special arrangements are necessary to prevent the thermometer being too much influenced by it. The instrument may be brought into close proximity to the deeper parts by being introduced into one of the mucous passages, where it is closely surrounded by vascular tissue. In animals the rectum is the most convenient part for the application of the thermometer, but in clinical practice it is usually placed under the tongue, or in the armpit, the bulb being held so that on all sides it is in contact with the skin and protected from the cool air.

The variations at different parts of the body are but slight, and the average normal surface temperature in man is found to be about 37° C.

Normal Variations in Temperature.

I. The temperature of *the whole body* normally undergoes certain variations, some of which are—1. Regular and periodical, depending upon the time of day, the ingestion of food, and the age of the individual. 2. Accidental, such as those caused by mental or bodily exertion.

a. The temperature is highest between 4 and 5 P.M. and lowest between 2 and 4 A.M., the transition being gradual. This diurnal variation, which normally does not much exceed 1° C., is much exaggerated in certain fevers.

b. The temperature rises after a hearty meal and falls during fasting. During starvation the temperature sinks gradually until the death of the individual.

c. The temperature is highest at birth, and falls about 1° C.

between that and the age of 50 years,—in extreme old age it is said that it again rises.

d. Muscular exertion, which gives the individual the sensation of great warmth, only changes the temperature of the blood about ·5° C. The very high temperature which accompanies the disease tetanus, where all the muscles are thrown into a state of spasm, probably depends more on pathological changes than on muscular action.

e. Mental exertion is also said to cause a rise of temperature.

f. Slight differences in the heat of the blood may be brought about by variations in the surrounding temperature. The abnormally high temperature of fever is much more easily affected by changes in the rate of removal of the heat from the body, than is the normal temperature, and hence the therapeutic value of cold applications in this class of disease.

II. The temperature of *different parts of the body* varies in a slight degree, and depends upon the following circumstances :—1. The amount of blood flowing through them ; the blood being the great carrier of warmth from one part to another, supplying heat where it is lost, and conveying material to those parts where the heat is generated. 2. The amount of heat produced, *i. e.*, the activity of its tissue change. 3. The amount of heat lost, which depends on (*a*) the extent of surface ; (*b*) the external temperature ; (*c*) the power of conduction of, and the capacity for heat of, the surrounding medium.

From this it is obvious that the deeper parts of the body, where active chemical change takes place, and which are protected from exposure, must be warmer than the exterior, which is constantly giving out its heat. The blood which flows through the surface vessels is cooled, and that which flows through the deeper vascular viscera is warmed. Thus the skin is usually about 37° C., while the mouth beneath the tongue is about 37·5° C., and the rectum about 38° C. The temperature of the blood therefore varies within narrow limits according to the part of the body through which it has recently passed. The mean temperature of the blood is higher than that of any tissue. The blood in the hepatic capillaries is the warmest in the body. This reaches 40·73° in the dog, or nearly two degrees higher than that in the aorta of that animal. The cool blood from the extremities and head mingling in the right side of the heart with the unusually warm blood from the liver keeps the blood going to the lungs at the standard temperature. The blood in the left side of the heart is a little cooler than that in the right, probably because the latter lies on the warm liver, as is proved by the substitution of

a cold object for this organ, when the blood on the right side becomes colder than the left. It is not because the blood is cooled going through the lungs, for the heat used in warming the respired air is given off by the nose and other air-passages, and not by the alveoli of the lungs.

III. The temperature *of an organ* varies with the state of its activity. During the active state the glands, &c. receive more blood and undergo more active chemical change, so that they become warmer.

Mode of Production of Animal Heat.

It has already been indicated that the general effect of the tissue change of the body is a kind of combustion in the tissues of certain substances obtained from the vegetable kingdom, viz., proteid, fat, carbo-hydrate, &c. The combustible substances are capable of being burned in the open air, or made to unite with oxygen so as to produce a certain amount of heat, being thus converted into CO_2 and H_2O. In the body the oxidation goes on in a gradual or modified way, and the end products of the process can be recognised as CO_2 eliminated from the lungs, and as water and urea got rid of by the kidneys. The general tendency of the chemical changes in the tissues is such as will set free energy in the form of heat.

The amount of heat that any substance is capable of giving off corresponds to the amount of energy required for the formation from CO_2 and H_2O, &c. of the compounds contained in it, and this correspondence remains whether the dissociation take place rapidly or slowly. The substances we make use of as food have thus a certain heat value which depends upon their chemical composition.

The high temperature which homœothermic animals can keep up in spite of the cold of the atmosphere in which they live is readily accounted for by the chemical change which is constantly occurring in the tissue of their bodies.

The amount of heat produced in any part depends upon the activity of its tissue change, for we find that the temperature varies with the elimination of CO_2, and urea, which gives a fair estimate of the normal chemical changes of the tissues.

1. The diurnal changes in temperature are accompanied by an afternoon increase and a morning decrease of CO_2 and urea.

2. The tissue change giving rise to CO_2 decreases in a fasting animal, as does also the production of heat.

3. More CO_2 is eliminated after meals, when the temperature also rises.

4. The activity of various organs, such as the muscles and glands, is associated with a local increase of temperature.

Income and Expenditure of Heat.

Income.—The chemical changes which give rise to heat, cause a certain waste of the tissues, which have again to be renewed by the assimilation of various nutrient materials. Food is thus the fuel of the animal body, and the peculiarity of the combustion is that the tissues assimilate or convert into their own substance the fuel, and then themselves undergo a kind of partial combustion by means of which they perform their several functions, amongst others heat-production.

As already mentioned, heat is produced most abundantly in those tissues which undergo most active chemical changes, hence the protoplasmic cells of glands and the contractile substance of muscle must be looked upon as the chief agents in setting heat free.

The possible heat-income depends on the amount of nutrient matter assimilated. As each kind of food has a certain heat value, *i. e.*, the number of heat-units its combustion will produce, we ought to be able to estimate the amount of heat produced by ascertaining this value and subtracting the calorific value of the various excreta, and the energy used in producing the muscular movements of the body. Since practically the temperature of the body remains the same, the amount of heat lost during a given time should correspond to the income estimated from the number of heat-units of the food. So far, however, attempts to make the calculated heat-income correspond with the expenditure have not been productive of satisfactory results, the calorific value of the food being hardly sufficient to produce the heat calculated to be given off, and the other work done by the body in the form of muscular movement, &c.

Since the activity of muscle and gland tissue is constantly undergoing variations in intensity, the amount of chemical change differs at different times, so that the amount of heat produced must also vary. We know that the heat set free by any organ, such as a gland or a muscle, increases in proportion to the increase of its functional activity, but we cannot say that the calorific activity can vary independently of other circumstances. Without such a special calorific function of some tissues, such as muscle, the actual net heat-income

must vary with circumstances which are accidental, and therefore irregular.

Since we know that the nervous system controls the tissue activities which are accompanied by the setting free of heat, we can see how the nerve-centres can materially influence the heat production of the body. The more active the muscles, glands, &c., which are under the control of nerves, the greater is the amount of heat produced in a given time. That the nervous system can cause in any tissue a chemical change, giving rise to a greater production of heat, without any other display of functional activity, we do not know, but many facts seem to point to such a possibility.

The effect of nerve influence on the production of heat is greatly complicated by the power exercised by the vaso-motor nerves over the blood supply to the great viscera, &c., for the temperature of any given part is so intimately related to the amount of blood flowing through it that the former has been accepted as an adequate measure of the latter.

For the present, therefore, we are not in a position to speak with decision of nerves with a purely thermic action.

The *Expenditure* of the heat may be classed under the following headings :

1. In warming ingesta : As a rule the food and drink we use as well as the oxygen we breathe are colder than the body, and before they pass out they are raised to the body temperature.

2. Radiation and Conduction : From the surface of the body a quantity of heat is being expended in warming the surrounding medium, which is habitually colder than our bodies. The colder the medium, the greater its capacity for heat, and the more quickly it comes in contact with new portions of the surface the more warmth it robs us of. Water or damp air takes up much more heat from our surface than dry air of the same temperature, and the quantity of heat lost is still further increased if the medium be in motion, so that the relatively colder fluid is constantly renewed.

3. Evaporation : (a.) From the larger air-passages : a quantity of water passes into the vaporous state and saturates the tidal air, and this change of condition from liquid to that of vapour absorbs much heat ; (b.) From the skin : surface evaporation is always going on, even when no moisture is perceptible on the skin, and much fluid of which we are not sensible is lost in this way. The quantity of heat lost by evaporation from the skin will depend on the temperature and the degree of moisture of the air in proportion to that of the surface of the body.

Balance.—As has been said, the exact income of heat is uncertain and variable because the data upon which the absolute amount can be calculated are not scientifically free from error. According to the most careful estimates an adult weighing 82 kilo. produces 2,700,000 units of heat in the twenty-four hours, which are expended in the following way :—

In warming ingesta . . .	70,157	units of heat.
In warming tidal air . . .	140,064	„ „
By the evaporation of 656 grm. of water from the air passages	397,536	„ „
By surface loss	2,092,243	„ „

From this it appears that more than three-quarters of our heat is lost by the skin (77·5 per cent.) ; by pulmonary evaporation, 14·7 per cent. ; in heating the air breathed, 5·2 per cent. ; in heating ingesta, 2·6 per cent.

Maintenance of Uniform Temperature.

In order that the vital processes of man and the other homœothermic animals should go on in a normal manner, it is necessary that their mean temperature remain nearly the same, and we have seen that under ordinary circumstances it varies only about one degree below or above the standard 37° C., notwithstanding the changes taking place in the temperature around us. Thus we can live in any climate, however cold or warm, and if our body temperature remains unaltered, we suffer no immediate injury.

There is a limit however to this power of maintaining a uniform standard temperature. If a mammal be kept for some time in a moist medium, where evaporation cannot take place, at a temperature but little higher than its body, say over 45° C., its temperature soon begins to rise and it dies with the signs of dyspnœa and convulsions (probably from the nervous centres being affected) when its temperature arrives at 43°—45°. If placed in water at freezing point an animal loses its heat quickly, and when its body temperature has fallen to about 20° C. it dies in a condition resembling somnolence, the circulation and respiration gradually failing.

Since a variation of more than one or two degrees in the temperature of our bodies interferes with the vital activities of the controlling tissue in the nervous centres, it is of course of the utmost importance that adequate means for the regulation of the mean temperature of our bodies should exist.

The temperature of an animal's body must depend on the relations existing between the amount of heat generated in the tissues and organs and the amount allowed to escape at the surface, and these must closely correspond in order that the heat of the body may remain uniform. Both these factors are found to be very variable. Every increase in the activity of the muscles, liver, &c., causes a greater production of heat, while a fall in external temperature or increase in the moisture of cool air causes a greater escape of heat from the surface.

The maintenance of uniform temperature may be accomplished by (1) variations in the heat income, so arranged as to make up for the irregularities of expenditure, or (2) variations in the loss to compensate for the differences of heat generated.

Since the temperature and moisture of our surroundings are constantly varying between tolerably wide limits, the amount of heat given off by our bodies must also vary. In cold damp weather a great quantity of heat is lost in comparison with that which escapes from the body when the air is dry or warm. If the heat generated had to make up for the changes in the heat lost, we should expect to find a correspondingly great difference in the amount of heat generated at different times of the year. No doubt we have some evidence in the keener appetite or use of more fuel, and the natural tendency to active muscular exertion during cold weather, to show that a greater amount of combustion takes place in winter than in summer. Further, if the preservation of a uniform body temperature depended solely upon the variations in the amount of income keeping pace with the variation in the expenditure, we should find it inconvenient to set our muscular or glandular tissues in action except when the external temperature was such as would enable us easily to get rid of the increased heat following their activity. It no doubt appears that the general tissue combustion, as measured by the amount of CO_2 given off, increases when we are placed in colder surroundings—such as a cold bath; still, it is probable that the variations in heat-income have but secondary regulating influence on the body temperature. If the rate of income have any regulating influence we are ignorant of the manner in which such influence is exerted, for it must act more slowly and cannot follow so closely, as the variations in expenditure do, extrinsic changes of temperature.

On the other hand, we know that the amount of heat-expenditure may be varied by mechanisms which are almost self-regulating. It has already been stated that the great majority of the heat is lost by the parts in contact with the air, namely, the skin and air passages.

In these places the warm blood is exposed to the cool air, and loses much of its heat by radiation, conduction, and evaporation. It is obvious that the greater the quantity of blood thus exposed for cooling the greater will be the amount of heat lost in a given time by the body as a whole.

If we review the circumstances which interfere with the uniformity of the temperature of the body, we shall see that each one is accompanied by certain physiological actions which tend to compensate for the disturbing influences.

The chief common events tending to make our temperature exceed or fall short of its normal standard may be enumerated as follows, and the explanation of their modes of compensation will at the same time be given:—

Compensation for internal Variations.

A casual increase in the heat income may be induced by any increased chemical activity in the tissues, notably the action of the muscles and large glands. When this increased heat is communicated to it, the warm blood, by the help of certain nerve centres, brings about the following results:—(*a.*) An acceleration of respiratory movement, increasing the amount of cold air to be warmed and saturated with moisture by the air passages, and facilitating the escape of the surplus caloric. (*b.*) Relaxation of the cutaneous arterioles, exposing a greater quantity of blood to the cooling influence of the air. (*c.*) Greater rapidity of the heart-beat, supplying a greater quantity of blood to the air passages and to the surface vessels. (*d.*) An increase in the amount of sweat secreted affording opportunity for greater surface evaporation.

As examples of these points may be mentioned active muscular exercise, which daily experience shows us is always accompanied by quick breathing, rapid heart's action, and a moist skin. The increased production of heat in fever gives rise to the same results, with the exception of the secretion of the sweat, which want (probably owing to the toxic inhibition of the special nerve mechanisms of the glands) is an important deficiency in the heat-regulating arrangements, and has much to do with the abnormally high temperature of the disease.

When a lesser quantity of heat is produced, owing to inactivity of the heat-producing tissues, the reverse takes place, namely, the respiration and heart's action are slow, the skin is pale and dry, so that little heat can escape.

Compensation for External Variations of Temperature.

When the temperature of the air rises much above the average, the escape of heat is correspondingly hindered ; and when the general body temperature begins to rise by this retention of caloric, we have the sequence of events detailed in the last paragraph. But before the blood can become warmer by the influence of the increased external temperature, the warm air, by stimulating the skin, brings about certain changes independent of the body temperature which satisfactorily check the tendency to an abnormal rise. This can be shown by the local application of external heat, by means of which (*a*) a rush of blood to the skin, and (*b*) copious sweat secretion may be induced in a part. This is brought about by impulses sent directly from the skin to the centres regulating the vasomotor and secretory mechanisms, and thus causing vascular dilatation and secretive activity. If a part only be warmed, a local effort is made to cool that part, and this has but little influence on the general body temperature.

When, however, the atmosphere becomes very warm, all the cutaneous vessels dilate simultaneously, and the escape of heat is greatly increased ; while, at the same time, so much blood being occupied in circulating through the skin the deeper—heat producing—tissues are supplied with less blood, and therefore generate a lesser quantity of heat. Thus a marked rise in the external temperature, which at first sight would seem to impede the escape of heat from the body, really facilitates it, by causing, through the vascular and glandular nerve mechanisms of the skin, a greater exposure of the blood to the cooler air, and a greater quantity of moisture to be evaporated from the warm skin. When the temperature of the air reaches that of the body, the only way of disposing of the heat generated in the body is by evaporation, for radiation and conduction become impossible. In animals like man, whose cutaneous moisture is great, external heat seldom causes marked change in the rate of breathing, but in animals whose cutaneous secretion is limited, external heat distinctly affects their respiratory movements, as may be seen by the panting of a dog on a very warm day, even when the animal is at rest.

Almost more important than facilitating the escape of heat in very warm weather, are the arrangements for preventing its loss when the surroundings are unusually cold. In this case the cold acting as a stimulus to the vaso-constrictor nerve agencies of the skin causes the blood to retire from the surface and fill the deeper organs, where

more heat is produced. This bloodless skin and the underlying fat then act as a non-conducting layer or boundary protecting the warm blood from the cooling exposure. At the same time the secretion of the sweat is controlled by a special nerve mechanism, which lessens evaporation and soon checks the secretion, thereby enabling the body to remain at the normal standard temperature.

It would then appear that the chief factors regulating the body temperature belong to the expenditure department, and may be said to be —(*a*) variation in the quantity of blood exposed to be cooled, and (*b*) variation in the quantity of moisture produced for evaporation.

These regulators have to compensate not only for differences of external temperature, but also for great fluctuations in the amount of heat produced in the tissues.

The regulating power of the skin, etc., appears to be adequate for the perfect maintenance of uniform temperature only within certain limits. When these limits are passed by the rise or fall in the surrounding medium, the preservation of a uniform temperature soon becomes impossible. These limits vary much in different animals, many of which have special coverings protecting them from external influences, and retain their warmth in a temperature seldom above 0° C. In man the limits vary according to many circumstances, *e.g.*, both extremes of age are more sensitive to changes of temperature. It would appear that for about 10° C. above and below the body temperature our skin-regulating mechanisms are adequate, but beyond these limits external changes affect our general temperature, and if continued become injurious. Of course by imitating with clothing the natural protection with which some animals are endowed we can aid the normal regulating factors, and bear much greater extremes of temperature with safety or even comfort.

It is somewhat surprising that our bodies are always at the same temperature, no matter how hot or cold we *feel*. This is quite true, and our sensations of being hot or cold are explained as follows :— When we feel hot our cutaneous vessels are full of warm blood, and this communicates to the cutaneous nerve terminals—the sensory nerves—the sensation of general warmth. On the other hand, when the cutaneous vessels are empty, the sensory nerves are directly affected by the cold of the external air. Since the full or empty state of the vessels of the skin depends generally on the heat or cold of the air, we use the expressions "it is hot or cold" and "we are hot or cold," as synonymous, because both ideas arise from the state of the skin. But we can make ourselves feel warm by violent exercise even on a frosty day, because we generate so much heat by muscular

action that the cutaneous vessels have to be dilated in order to get rid of the surplus, and our skin vessels being full we feel warm. Our feelings when we say we are warm or cold simply depend upon our cutaneous vessels being full or empty of warm blood.

The local appreciation of differences of temperature will be discussed in the chapter dealing with the sense of Touch.

CHAPTER XXV.

CONTRACTILE TISSUES.

In the lower forms of organisms the motions executed by protoplasm suffice for all their requirements. Thus the amœba manages to pass through its lifetime with no other kind of motion at its disposal than the flowing circulation and the budding out of its soft protoplasm. A vast number of minute organisms depend wholly upon the protoplasmic stream and the twitching of cilia for their digestive and progressive movements. Before we leave the class of animals which never pass beyond the unicellular stage, we find, however, examples in which a portion of their protoplasm is specially adapted to the performance of sudden and rapid motions. The protoplasm so modified in function deserves the name of contractile material. Thus, though the protoplasm which lies within the stalk of the bell animalcule is morphologically undifferentiated, it can contract with such rapidity that the eye cannot follow the motion.

As we ascend in the scale of animal life, the necessity for motions of varied rapidity and duration at the command of the animal becomes more and more urgent, and so we find not only one, but several kinds of tissue specially adapted for carrying out motions of different rate and duration.

As a general rule the more rapid the contraction it performs the more the tissue differs from the original type of protoplasm; and the slower and more persistent the contraction, the more the tissue elements resemble protoplasmic cells. Thus, in the minute blood-vessels, as we have seen, a very prolonged form of contraction, only varied by partial relaxations, is the rule, and gives rise to the tone of the arterioles, and the contractile elements differ but little from ordinary protoplasmic cells. The intestinal movements are rapid compared with those of the arterial muscles, and in them we find a thin, elongated form of muscle cell. In the heart a forcible and quick contraction takes place, which, however, is slow when compared with the sudden jerk of a single spasm of a skeletal muscle, and its texture is different, being a form intermediate between the slow-

contracting smooth muscle and the quick-contracting striated skeletal muscle.

By borrowing examples from the lower animals, this parallelism of structural differentiation and increase of functional energy can be more perfectly demonstrated, and we can make out a gradual scale of increasingly rapid motion corresponding with greater complexity of structure.

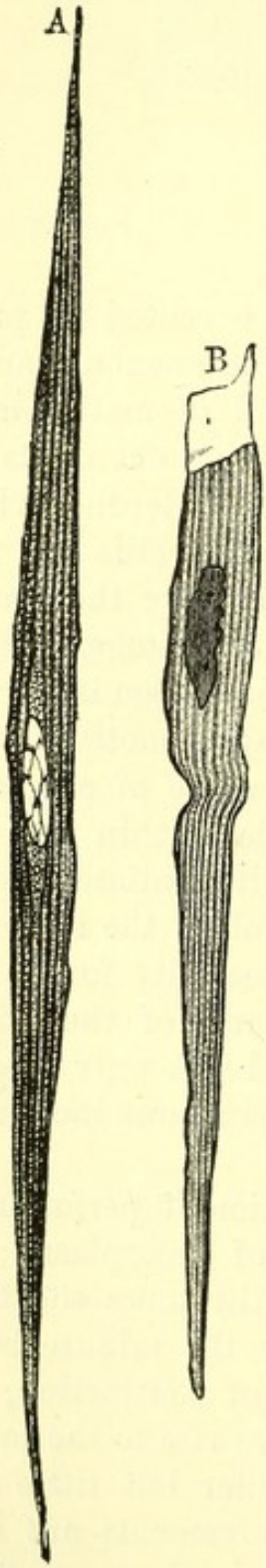


Fig. 177.—Muscle cells, showing different condition of the protoplasm of the cell and nucleus.

Histology of Muscle.

The term muscle includes the textures in which the protoplasm is specially differentiated for purposes of contraction.

The muscle tissues of the higher animals may be divided into two classes ; 1. non-striated or smooth, and 2. striated, in which again there are some slight variations.

The *non-striated muscle tissue* is that in which the elements are most like contractile protoplasmic cells, and have so far retained the typical form as to be easily recognisable as cells when separated one from the other. These cells are more or less elongated, flattened, homogeneous elements with a single, long, rod-shaped nucleus and no cell wall. They are tightly cemented together by a tough elastic substance, so that their tapering extremities fit closely together and form commonly a dense mass or sheet. Sometimes they branch more or less regularly, and then are arranged in net-works.

These cells vary greatly in size as well as in the relation of their length to their width, in some places deserving the name fibres, or fibre-cells, and in others being only elongated cells.

The *striated muscle tissue* is that of which the skeletal muscles and the heart are composed. It therefore forms the larger proportion of the animal, known as the flesh. The flesh can by judi-

cious dissection easily be divided into single parts called muscles, each of which contains many other tissues and is so attached as to carry on certain movements, and may, therefore, be regarded as an organ.

Such a muscle is enclosed in a sheath of connective tissue, from which sheet-like partitions or septa pass into the mass of the muscle and divide it into bundles of fibres, which they enclose. These septa also act as the bed in which the vessels and nerves lie.

The tissue of the heart differs from other striated muscle in being made up of truncated oblong branching cells with a central nucleus and no sarcolemma (see page 214).

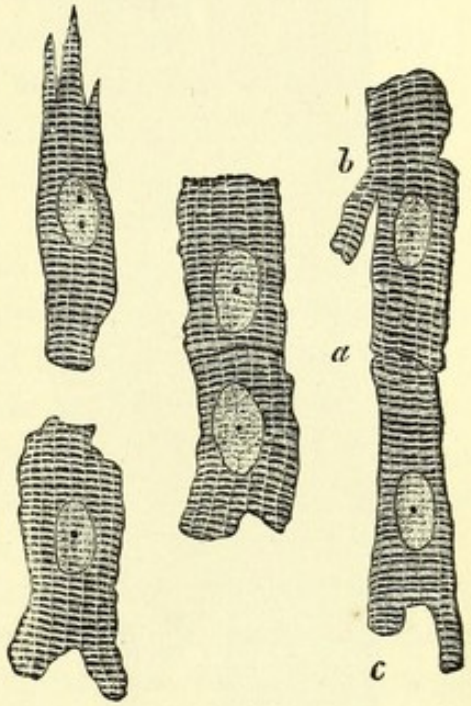


Fig. 178.—Short striated cells of the *heart-muscle*, separated one showing the truncated (*a*), or divided (*c*), ends and branches (*b*).

The bundles of fibres of *skeletal muscle* vary much in size, giving a coarse or fine grain in different muscles ; they are composed of a greater or less number of fibres, which lying side by side run parallel one to the other. The single fibres of striated muscle vary in length, sometimes reaching 4—5 cm. (2 inches), but being on an average much shorter, they only extend the entire length of a muscle in the case of very short muscles. In long muscles their tapering points are made to correspond with those of other fibres to which they are firmly attached. The soft fibres are pressed by juxtaposition into prismatic forms, so that in a fresh condition they appear polygonal in transverse section. When freed from all pressure or traction they become cylindrical, and the transverse striation of the contractile substance appears regular, and is easily recognised.

Each fibre consists of a delicate case of thin, elastic, homogeneous membrane, forming a sheath called *sarcolemma*, within which the essential contractile substance is enclosed. The soft contractile substance completely fills and distends the elastic sarcolemma, so that when the latter is broken its contents bulge out or escape. After death, particularly if preserved in weak acid (HCl), the striation becomes more marked, and the dead and now rigid contractile substance can be easily broken up into transverse plates or discs.

Besides the traverse striation a longitudinal marking can be seen in the muscle fibre which indicates the subdivision of the contractile

substance into thin threads called primitive fibrillæ. Each primitive fibril shows a transverse marking, corresponding with the transverse striation, which divides the fibrils into short blocks called sarcous, or muscle elements. These markings, and the transverse striations of the muscle fibre in general, depend on different parts of the contractile substance having different powers of refraction, and giving the appearance of dark and light bands.

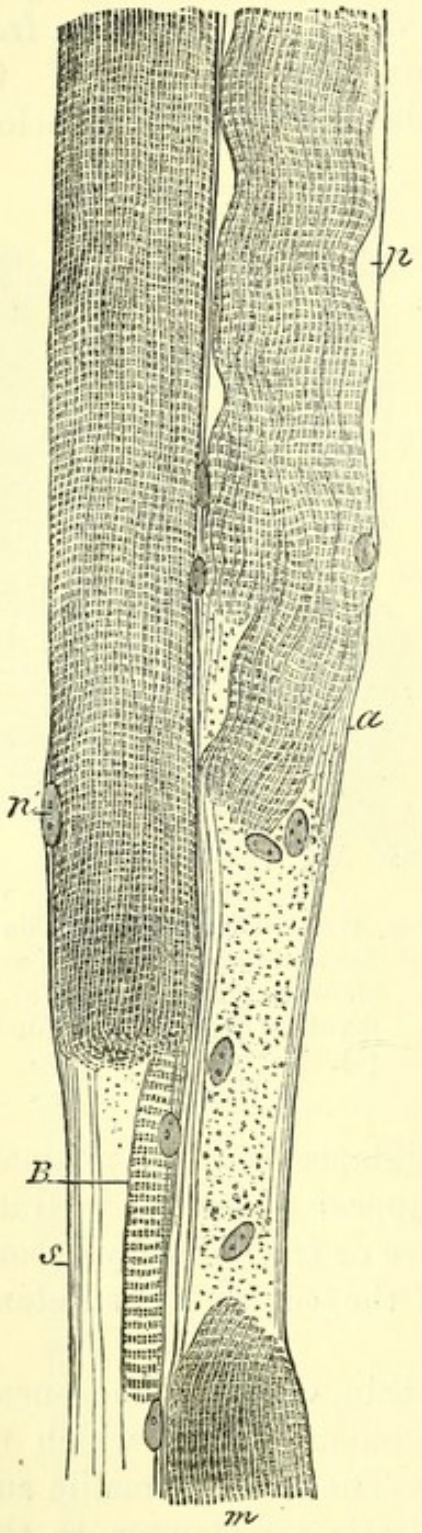


Fig. 179.—Two fibres of striated muscle, in which the contractile substance (*m*) has been ruptured and separated from the sarcolemma (*a*) and (*s*); (B) shows a thin strip of torn contractile substance in which the transverse markings are clearer; (*n*) nuclei, (*p*) space under sarcolemma. (Ranvier.)

In the muscle fibre are found long granular masses like protoplasm; these are the nuclei of the contractile substance. They must not be confounded with the nuclei of the sarcolemma, which are much more numerous along the edge of the fibre, or with the other short nuclei seen in such numbers between the fibres, which indicate the position of the capillary vessels.

It is stated that each striated muscle fibre has a nerve fibre passing directly into it, but the exact details of the mode of union in mammalia are not yet satisfactorily made out.

Properties of Muscle in the Passive State.

Consistence.—The contractile substance of muscle is so soft as to deserve rather the name fluid than solid; it will not drop as a liquid, but its separated parts will flow together again like half-melted jelly. In this respect it resembles the protoplasm of some elementary organisms, the buds from which are so soft that they can unite around

foreign bodies, and yet have sufficient consistence to distinguish them from fluid.

Chemical composition.—The chemical constitution of the contractile substance of muscle in the living state is not accurately known. The death of the tissue is accompanied by certain changes of a chemical nature which give rise to a kind of coagulation, resulting in the formation of two substances, viz., *muscle serum* and *muscle clot* or *myosin*. This coagulation can be postponed almost indefinitely in the contractile substance of the muscles of cold-blooded animals, by keeping the muscle after its removal at about 5° C. In this way a pale yellow, opalescent, alkaline juice may be pressed out of the muscle and separated on a cold filter. This substance turns to a jelly at freezing point, and if brought to the ordinary temperature of the room it passes through the stages of coagulation seen in the contractile substance of dead muscle, and gives the same fluid serum and clot of myosin. Since a frog's muscle can be frozen and thawed without the tissue being killed, it is supposed that the thick juice is really the contractile substance, which has been called *muscle plasma*.

The coagulation of muscle plasma reminds us in many ways of the clotting of the blood plasma, but the muscle-clot, or myosin, is gelatinous and not in threads like fibrin. It is a *globulin*, and is soluble in 10 per cent. solution of salt. It is readily changed into syntonin or acid albumin, and forms the preponderant albuminous substance of muscle.

The serum of dead muscle has an acid reaction, and contains three distinct albuminous bodies coagulating at different temperatures, one of which is serum-albumin, and another a derived albumin, potassium-albumin. The serum of muscle also contains: (1.) Kreatin, kreatinin, xanthin, &c. (2.) Hæmoglobin. (3.) Grape sugar, muscle sugar, of inosit, and glycogen. (4.) Sarcolactic acid. (5.) Carbonic acid. (6.) Potassium salts; and (7.) 75 per cent. of water. Traces of pepsin and other ferments have also been found.

Chemical change.—In the state of rest a certain amount of chemical change constantly goes on, by which oxygen is taken from the hæmoglobin of the blood in the capillaries, and carbonic acid is given up to the blood. These changes seem necessary for the nutrition, and therefore the preservation of the life and active powers of the tissue, because if a muscle after removal be placed in an atmosphere free from oxygen, it more quickly loses its chief vital character, viz., its irritability.

Elasticity.—Striated muscle is easily stretched, and, if the extension

be not carried too far, recovers very completely its original length. That is to say, the elasticity of muscle is small or weak, but very perfect. When a muscle is stretched to a given extent by a weight —say of 1 gramme—if another gramme be then added, it will not stretch the muscle so much as the first did; and so on if repeated gramme weights be added one after the other, each succeeding

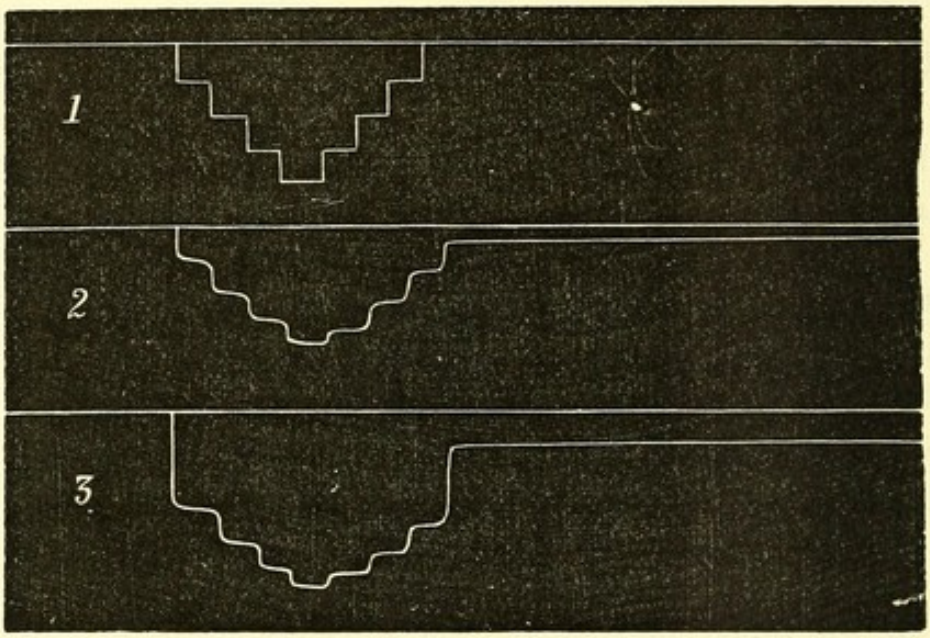


Fig. 180.—1. Shows graphically the amount of extension caused by equal weight increments applied to a steel spring.
2. Shows graphically the amount of extension caused by equal weight increments applied to an india-rubber band.
3. The same applied to a frog's muscle. Showing the decreasing increments of extension; the gradual continuing stretching and the failure to return to the abscissa when the weight is removed.

gramme will cause less extension of the muscle than the previous one; so that the more a muscle is stretched the more force is required to stretch it to the given extent, or, in other words, the elastic force of muscle increases with its extension.

If a tracing be drawn showing the extending effect of a series of equal weights attached to a fresh muscle, it will be found that a great difference exists between it and a similar record drawn by inorganic bodies or an elastic band of rubber.

When a weight is applied to a muscle, it does not immediately stretch to the full extent the weight is capable of effecting, but a certain time, which varies with circumstances, is required for its complete extension. The rate of extension is at first rapid, then slower, until it ceases. As a muscle loses its powers of contraction from fatigue, it becomes more easily extended. Dead muscle has a greater but less perfect elasticity than living, *i.e.*, it requires greater

force to stretch it, but does not return so perfectly to its former shape. The importance of the elastic property of muscle in the movements of the body is noteworthy. The muscles are always in some degree on the stretch (as can be seen in a fractured patella, the fragments of which remain far apart and cause the surgeon much anxiety), and brace the bones together like a series of springs, the various skeletal muscles being so arranged as to stretch others by their contraction. When one muscle—for example, the biceps—contracts, it finds an elastic antagonist already tense, and has to shorten this antagonist as it contracts itself. The triceps in this case acts as a weak spring, opposing the biceps, and it gently returns to its natural length when the contraction of the biceps ceases. The muscles are kept tense and ready for action by their mere elasticity, and have to act against a gentle spring-like resistance, so that the motions occur evenly, and there is no jarring or jerking, as might take place if the attachments of the inactive muscles were allowed to become slack.

Electric Phenomena.—In a living muscle electric currents may be detected, having a definite direction, and certain relations to the

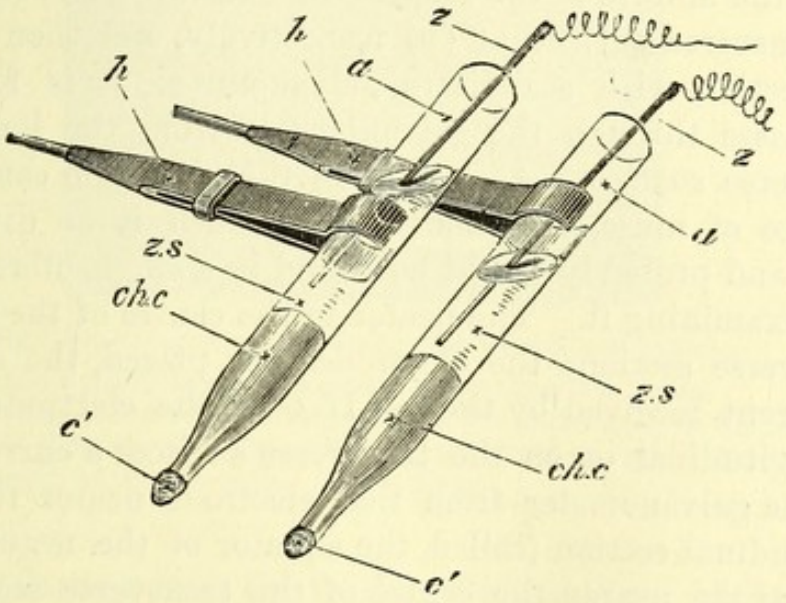


Fig. 181.—Non-polarisable Electrodes. The glass tubes (*a a*) contain sulphate of zinc solution (*z. s*), into which well amalgamated zinc rods dip. The lower extremity is plugged with china clay (*ch. c*), which protrudes at (*c'*) the point. The tubes can be moved in the holders (*h h*), so as to be brought accurately into contact with the muscle. (Foster.)

vitality of the tissue. As they seem to be invariably present in a passive muscle they have been called *natural muscle currents.*

They are generally studied in the muscles of cold-blooded animals after removal from the body. The muscle is spoken of as if it were a cylinder with longitudinal and transverse surfaces corresponding

to its natural surface and its cut extremities. In such a block of frog's muscle the measurement of the electric currents requires considerable care, because they are so difficult to detect that a most sensitive galvanometer must be used; and such an instrument can easily be disturbed by currents due to bringing metal electrodes into contact with the moist saline tissues. Specially constructed electrodes must be used to avoid these currents of polarisation taking place in the terminals touching the muscle. These are called *non-polarisable electrodes*, and may be made on the following plan:— Some innocuous material moistened in saline solution (·65 per cent.) is brought into direct contact with the muscle, and, by means of saturated solution of zinc sulphate, into electrical connection with amalgamated zinc terminals from the galvanometer. Thus the muscle is not injured, and the zinc solution prevents the metal terminals from producing adventitious currents.

Small glass tubes drawn to a point, the opening of which is plugged with china clay moistened with salt solution, make a suitable receptacle for the zinc solution. If a pair of such electrodes be applied to the middle of the longitudinal surface at (*e*) (fig. 182), and of the transverse surface at (*p*) respectively, and then be brought into connection with a delicate galvanometer, it is found that a current passes through the galvanometer from the longitudinal to the transverse surface. A current in this direction can be detected in any piece of muscle, no matter how much it be divided longitudinally, and probably would be found in a single fibre had we the means of examining it. The nearer to the centre of the longitudinal and transverse sections the electrodes are placed, the stronger will be the current received by them. If both the electrodes be placed on the longitudinal or on the transverse surfaces a current will pass through the galvanometer from that electrode nearer the middle of the longitudinal section (called the equator of the muscle cylinder) to the electrode nearer the centre of the transverse section (pole of muscle cylinder). If the electrodes be placed equidistant from the poles or from the equator no current can be detected.

The central part of the longitudinal surface of a piece of muscle is then positive, compared with the central part of the extremities or transverse sections. And between these parts, the equator and poles of the muscle cylinder, where the difference is most marked, are various gradations, so that any point near the equator is positive when compared with one near the poles.

There is, then, a current passing through the substance of the piece of muscle from both the transverse sections or extremities of

the muscle block to the middle of the longitudinal surface, whether it be a cut surface (longitudinal section) or the natural surface of the muscle. This is called the *muscle current*, or sometimes *natural muscle current*.

If the cylinder in the accompanying figure be taken to represent a block of muscle, *e* would correspond to the equator, and *p* to the poles, and the arrowheads show the direction of the currents passing

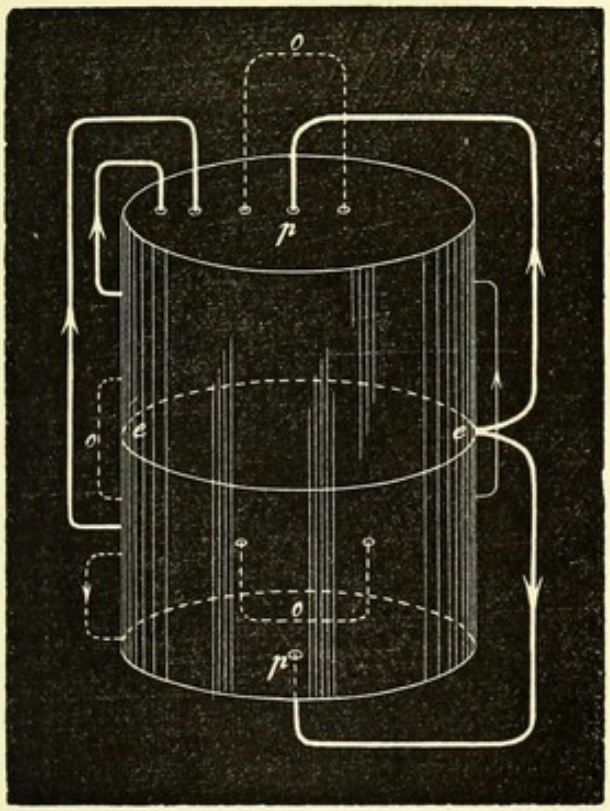


Fig. 182.—Diagram to illustrate the currents in muscle.

(*e*) Equator, corresponds to the centre of the muscle cylinder.

(*p*) Polar regions of cylinder representing the extremities of the mnscle.

The arrow heads show the direction of the surface currents, and the thickness of lines indicates the strength of the currents. (After Fick.)

through the galvanometer, the thickness of the lines indicating their force. The dotted lines *o* are connected with points where the electro-motive force is equal, and therefore no current exists.

The electro-motive force of the muscle-current in a frog's gracilis has been estimated to be about ·05—·08 of a Daniell cell. It gradually diminishes as the muscle loses its vital properties, and is also reduced by fatigue. The electro-motive force rises with the temperature from 5° C. until a maximum is reached at about the body temperature of mammals.

These muscle-currents are very weak if the uninjured muscle be examined *in situ*, the tendon being used as the transverse section; they

soon become more marked after the exposure of the muscle, and if the tendon be injured they appear at once in almost full force. In animals quite inactive from cold the muscles naturally are but slowly altered by exposure, &c., and the muscle-currents do not appear for a considerable time, which is shortened on elevating the temperature. It has, therefore, been supposed that in the perfectly normal state of a living animal there are no muscle currents so long as the muscle remains in the passive state.

Active State of Muscle.

A muscle is capable of changing from the passive elongated condition, the properties of which have just been described, into a state of contraction or activity. Besides the change in form, obvious in the contracted state of the muscle, its chemical, elastic, electric, and thermic properties are altered. The capability of passing into this active condition is spoken of as the *irritability* of muscle. This is directly dependent upon its chemical condition, and therefore related to its nutrition and to the amount of activity recently exerted, which, as will hereafter appear, changes its chemical state.

Under ordinary circumstances, during life, the muscles change from the passive state into that of contraction in response to certain impulses communicated to them by nerves, which carry impressions from the brain or spinal cord to the skeletal muscles. The influence of the will generally excites most skeletal muscles to action. Nearly all muscular contraction depends on nervous impulses of one kind or another. But there are many other influences which, when applied to a muscle, can bring about the same change. These influences are called *stimuli*.

We utilise the nerve belonging to a muscle in order to throw it into the contracted state, but the great majority of stimuli can bring about the change when applied to the muscle directly. Since the nerves branch in the substance of the muscle, and are distributed to the individual fibres, it might, as has been argued, be the stimulation of the terminal nerve ramifications that brings about the contraction, even when the stimulus is applied to the muscle directly, for the terminal branches of the nerves are affected by the stimulus applied to the muscle.

That muscles can be stimulated without the intervention of nerves is satisfactorily proved by the following facts :—

1. Some parts of muscles, such as the lower end of the sartorius,

and many muscular structures which have no nerve terminals in them, respond energetically to all kinds of muscle-stimuli.

2. There are some substances which act as stimuli when applied directly to muscle, but have no such effect upon nerves, viz., ammonia.

3. For some time after the nerve has ceased to react, on account of its dying after removal from the body, the attached muscle will be found quite irritable if directly stimulated.

4. The arrow-poison, *Curara*, has the extraordinary effect of paralysing the nerve terminals, so that the strongest stimulation of the nerve calls forth no muscle contraction. If the muscles in an animal under the influence of this poison be directly stimulated, they respond with a contraction.

Muscle-Stimuli.

The circumstances which call forth muscle contraction may be enumerated thus :—

1. *Mechanical Stimulation.*—Any sudden blow, pinch, &c., of a living muscle causes a momentary contraction, which rapidly passes off when the irritation is removed.

2. *Thermic Stimulation.*—If a frog's muscle be warmed to over 30° C. it will begin to contract, and before it reaches 40° C. it will pass into a condition known as heat rigor, which will be mentioned presently. If the temperature of a muscle be reduced below 0° C. it shortens before it becomes frozen.

3. *Chemical Stimulation.*—A number of chemical compounds act as stimuli when they are applied to the transverse section of a divided muscle. Among these may be named—(1) the mineral acids (HCl, ·1 per cent.) and many organic acids ; (2) salts of iron, zinc, silver, copper, and lead ; (3) the neutral salts of the alkalies of a certain strength ; (4) weak glycerine and weak lactic acid ; these substances only excite nerves when concentrated ; (5) bile is also said to stimulate muscle in much weaker solutions than it will nerve fibres.

4. *Electric Stimulation.*—Electricity is the most convenient form of stimulation, because we can accurately regulate the force of the stimulus. The occurrence of variation in the intensity of an electric current passing through a muscle causes it to contract. The sudden increase or decrease in the strength of a current acts as a stimulus, but a current of exactly even intensity may pass through a muscle without further exciting it, after the initial contraction has ceased. A common method of producing such a variation is that of opening or closing

an electric circuit of which the muscle forms a part, so as to *make* or *break* the current; and thus a variation of intensity equal to the entire strength of the current takes place in the muscle, and acts as a stimulus.

The direct current from a battery (*continuous current*) is used to

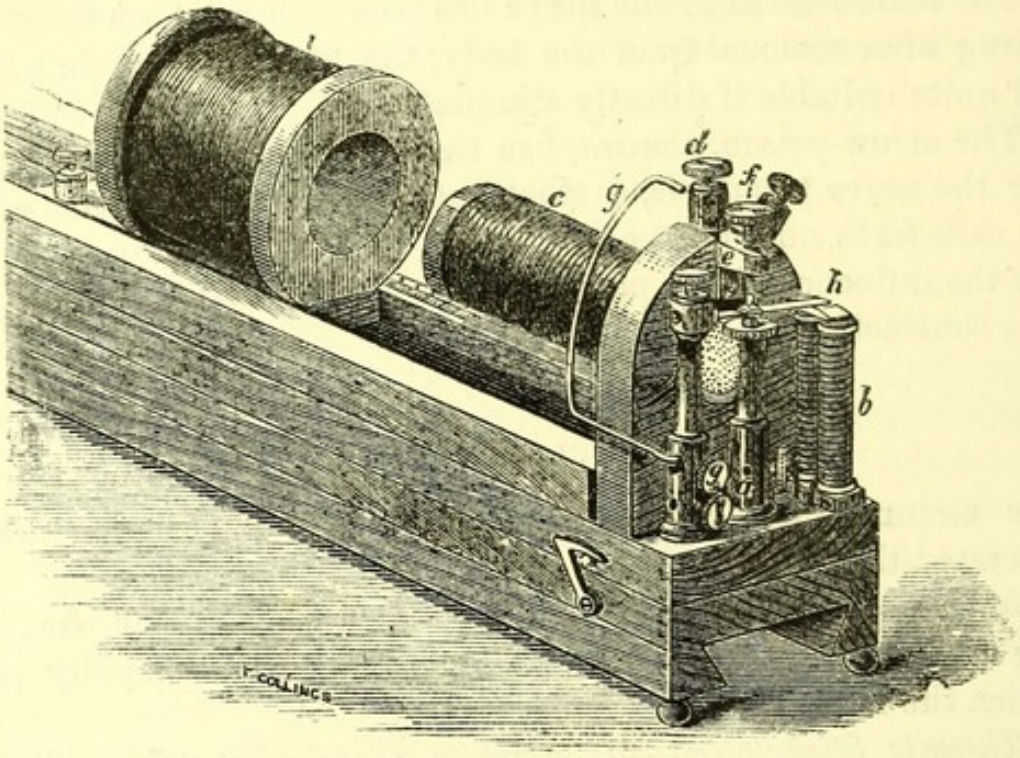


Fig. 183.—Du Bois Reymond's Inductorium with Magnetic Interrupter.

c. Primary coil through which the primary, *inducing*, current passes, on its way to the electro-magnet (*b*).

i. Secondary coil, which can be moved nearer to or further from the primary coil (*c*), thereby allowing a stronger or weaker current to be induced in it. This *induced* current is the stimulus.

b. Electro-magnet, which on receiving the current breaks the contact in the circuit of the primary coil by pulling down the iron hammer (*h*), and separating the spring from the screw of *e*. When using Helmholtz's modification (*g'*), (*e*) is screwed up and the current brings the spring in contact with the point of the pillar (*a*), and so demagnetises (*b*) by "short-circuiting" the battery.

When tetanus is to be produced, the wires from the battery are to be connected with *g* and *a*.

When a single contraction is required, the magnetic interrupter is cut out by shifting the wire from *a* to the binding screw to the right of *f*.

stimulate a muscle in certain cases, but a current induced in a secondary coil by the entrance or cessation of a current in a primary coil of wire (*induced current*) is more commonly employed on account of the greater efficacy of its action. The instrument used for this purpose in physiological laboratories is Du Bois-Reymond's inductorium, in which the strength of the stimulus can be reduced by removal of the secondary coil from the primary. It is supplied with a magnetic interrupter by means of which repeated stimuli may be given by

rapidly making and breaking the primary current (*interrupted current*) (Fig. 183.)

The irritability of muscle-substance is not so great as that of the motor nerves, that is to say, a less stimulus applied to the nerve of a nerve-muscle preparation* will cause contraction than if applied to the muscle directly. In experimenting on the contraction of muscle, as already stated, the nerve is commonly used to convey the stimulus, because when an electric current is applied to the nerve, the stimulus is the more safely and completely distributed throughout the muscle fibres than when it is applied directly.

Changes occurring in Muscle on its entering the Active State.

Changes in Structure.—The examination of muscle with the microscope during its contraction is attended with considerable difficulty, and in the higher animals has not led to satisfactory results. In the muscles of insects, where the differentiation of the contractile substance is more marked, certain changes can be observed. The fibres, and even the fibrillæ within them, can easily enough be seen to undergo changes in form corresponding to those of the entire muscle, namely, increase in thickness and diminution in length. A change in the position and relative size of the singly and doubly refracting portions of the muscle element has been described, and some authors state that the latter increases at the expense of the former after an intermediate period in which the two substances seem fused together.

Chemical Changes.—During the contracted condition the chemical changes which go on in passive muscle are intensified, and certain new chemical decompositions arise of which not much is known.

Active muscle takes up more oxygen than muscle at rest, as is shown by the facts that, during active muscular exercise, more oxygen enters the body by respiration, and the blood leaving active muscles is poorer in oxygen than when the same muscles are passive. This absorption of oxygen may be detected in a muscle cut out of the body, but a supply of oxygen is not necessary for its contraction, since an excised frog's muscle will contract in an atmosphere containing no oxygen. From this it would appear that a certain ready store of oxygen must exist in some chemical constituent of the muscle substance. It is possible that some chemical compound,

* By a nerve-muscle preparation is meant a muscle of a frog (commonly the gastrocnemius and the half of the femur to which it is attached) and its nerve which have been carefully separated from other parts and removed from the body.

constantly renewed by the blood, is the normal source of oxygen, and not the oxy-hæmoglobin.

The amount of CO_2 given off by a muscle increases in its state of activity. This may be seen (α) by the greater elimination from the lungs during active muscular exercise, and (β) by the fact that the venous blood of a limb, when the muscles are contracted, contains more CO_2 than when they are relaxed. (γ) The increase of CO_2 can also be detected in a muscle removed from the body and kept in a state of contraction. (δ) This increase in the formation of CO_2 takes place whether there is a supply of oxygen or not, (ϵ) and the quantity of CO_2 given off exceeds the quantity of oxygen that is used up. So that it is not exclusively from the newly-supplied oxygen that the CO_2 is produced.

Muscle tissue, when passive, is neutral or faintly alkaline ; during contraction, however, it becomes distinctly acid. The litmus which it changes from blue to red is permanently altered, and the conclusion follows that CO_2 is not the only acid that makes its appearance. The other acid is *sarcolactic acid*, which is constantly present in muscle after prolonged contraction, and varies in amount in proportion to the degree of activity the muscle has undergone. If artificial circulation be kept up in the muscle the quantity of sarcolactic found in the blood is very great. It varies directly with the CO_2, which would seem to suggest a relationship between the origin of the two acids.

The amount of glycogen and grape sugar is said to diminish in muscle during its activity, and it is stated that sarcolactic acid can be produced from these carbo-hydrates by the action of certain ferments.

Active muscle contains more of those substances that can be extracted by alcohol and less that are soluble in water than passive muscle.

The chemical changes which take place during muscle contraction are probably the result of a decomposition of some carbo-hydrates, in which the albuminous substances do not take any part that requires their own destruction. This seems supported by the fact that the increased gas exchange in muscle during active exercise can be recognised in a corresponding alteration in the gas exchange in pulmonary respiration ; and there seems no relation between muscular labour and the amount of nitrogenous waste, as estimated by the urea elimination, which we should expect if muscular activities were the outcome of a decomposition of the nitrogenous (albuminous) parts of the muscle substance.

The chemical changes, then, said to take place in muscle during its *contraction* are :—

1. The contractile substance, which is normally neutral or faintly

alkaline, become acid in reaction owing to the formation of sarcolactic acid.

2. More oxygen is taken up from the blood than when the muscle is at rest. This using up of oxygen occurs also in the isolated muscle, and its amount appears to be independent of the blood supply.

3. The extractives soluble in water decrease, those soluble in alcohol increase.

4. A greater amount of CO_2 is given off, both in the isolated muscle and in the muscles in the body, and the change in the quantity of CO_2 has no exact relation to that of the oxygen used.

5. A diminution is said to occur in the contained glycogen, and certainly prolonged inactivity causes an increase in the amount of glycogen.

6. A peculiar muscle-sugar makes its appearance.

I. *Change in Elasticity.*—The elasticity of a muscle during its state of contraction is less than in the passive state. That is to say a given weight will extend the same muscle more if attached to it while contracted (as in tetanus) than when it is relaxed. The contracted muscle is then more extensible. If a weight which is just over the maximum load the muscle can lift, be hung from it and the muscle stimulated, it should become extended, because the change to the active state lessens its elastic power, while it cannot contract, being over-weighted.

II. *Electrical Changes.*—If a muscle, in connection with a galvanometer so as to show the natural current, be stimulated by means of the nerves, a marked change occurs in the current. The galvanometric needle swings towards zero, showing that the current is weakened or destroyed. This is called the *negative variation* of the muscle current which initiates the change to the active condition. When the muscle receives but a momentary stimulus sufficient to give a single contraction, this negative variation takes place in the current, but, owing to its extremely short duration, the galvanometric needle is prevented by its inertia from following the change. Only the most sensitive and well-regulated instruments show the electric change of a single contraction, but when the muscle is kept contracted by a series of rapidly repeated stimulations the inertia of the needle is readily overcome.

Rheoscopic Frog.—The negative variation of a single contraction can be easily shown on the sensitive animal tissues. For this purpose the sciatic nerve of a frog's leg is placed upon the surface of the gastrocnemius of another leg, so as to pass over the middle and the extremity

of the muscle. When the second (stimulating) muscle is made to contract, its negative variation acts as a stimulus to the nerve lying on it, and so the first (stimulated) muscle contracts. Not only does this show the negative variation of a single contraction, but it also demonstrates that the continued (tetanic) contraction, produced by interrupted electric stimulation, is associated with repeated negative variations. We shall see that the continued contraction is brought about by a rapidly repeated series of stimulations, so that the electric condition of the stimulating muscle undergoes a series of

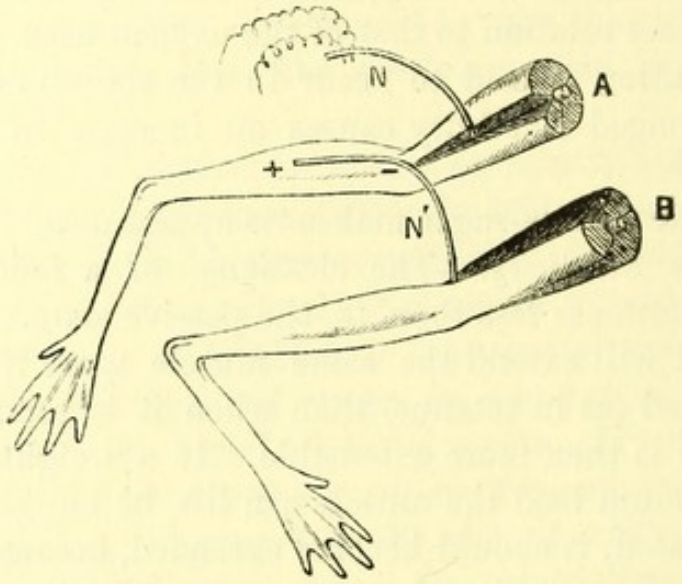


Fig. 184.—Diagram illustrating the arrangement in the Rheoscopic Frog.

A = *stimulating* limb. B = *stimulated* limb. The current from the electrodes passes into nerve (N) of stimulating limb (A), causing its gastrocnemius to contract. Whereupon the negative variation of the natural current between + and − stimulates the nerve (N'), and excites the muscles of B to action.

variations. The contraction of the *stimulated* muscle, whose nerve lies on the *stimulating* muscle, responds to the electric variations of the stimulator, and contracts synchronously with it.

If an isolated part of a muscle be stimulated, the contraction passes from that point as a wave to the remainder of the muscle. This contraction wave is preceded by a wave of negative variation which passes along the muscle at the rate of 3 metres per second (the same rate as the contraction wave), lasting at any one point ·003 of a second, so that the negative variation is over before the contraction begins, for the muscle requires a certain time, called the latent period, before it commences to contract.

The origin of the electric currents of muscle will be discussed with nerve-currents, to which the reader is referred.

III. *Temperature Change.*—Long since it was observed in the human subject that the temperature of muscles rose during their

activity. In frogs' muscle a contraction lasting 3 minutes caused an elevation of ·18° C. A single contraction is said to produce a rise varying from ·001° to ·005° C., according to circumstances.

The production of heat is in proportion to the tension of the muscle. When the muscles are prevented from shortening, a greater amount of heat is said to be produced.

The amount of heat has also a definite relation to the work performed. Up to a certain point the greater the load a muscle has to move, the greater the heat produced; when this maximum is reached any further increase of the weight causes a falling off in the heat production. Repeated single contractions are said to produce more heat than tetanus kept up for a corresponding time.

The fatigue which follows prolonged activity is accompanied by a diminution in the production of heat.

IV. *Change in form.*—The most obvious change a muscle undergoes in passing into the active state is its alteration in shape. It becomes shorter and thicker. The actual amount of shortening varies according to circumstances. (*a*) A muscle on the stretch when stimulated will shorten more in proportion than one whose elasticity is not called into play before contraction, so that a slightly weighted muscle shortens more than an unweighted one with the same stimulus. (*b*) The fresher and more irritable a muscle is, the shorter it will become in response to a given stimulus; and, conversely, a muscle which has been some time removed from the body, or is fatigued by prolonged activity, will contract proportionately less. (*c*) With a certain limit, the stronger the stimulus applied the shorter a muscle will become. (*d*) A warm temperature augments the amount of shortening, the amount of contraction of frogs' muscles increasing up to 33° C. A perfectly active frog's muscle shortens to about half its normal length. If much stretched and stimulated with a strong current it may contract nearly to one fourth of its length when extended. Muscles are seldom made up of perfectly parallel fibres, the direction and arrangement varying much in different muscles. The more parallel to the long axis of the muscle the fibres run, the more will the given muscle be able to shorten in proportion to its length.

The thickness of a muscle increases in proportion to its shortening during contraction, so that there is but little change in bulk. It is said, however, to diminish slightly in volume, becoming less than $\frac{1}{1000}$th smaller. This can be shown by making a muscle contract in a bottle filled with weak salt solution so as to exclude all air and to communicate with the atmosphere only by a capillary tube into which

the salt solution rises. The slightest decrease in bulk is shown by the fall of the thin column of fluid in the tube.

Since a muscle loses in elastic force and gains but little in density during contraction, the hardness which is communicated to the touch depends on the difference of tension of the semi-fluid contractile substance within the muscle sheath.

The Graphic Method of Recording Muscle Contraction.

In order to study the details of the contraction of muscle, the graphic method of recording the motion is applied. The curve may be drawn on an ordinary cylinder moving sufficiently rapidly. Where accurate time measurements are required it is better to use one of the many special forms of instruments, called *myographs*, made for the purpose. The principle of all these instruments is the same ; namely, an electric current, which passes through the nerve of a frog's muscle connected with the marking lever, is broken by some mechanism, while the surface is in motion ; the exact moment of breaking the contact can be accurately marked on the recording surface, by the lever which draws the muscle curve, before the instrument is set in motion. The rate of motion is registered by a tracing drawn by a tuning fork of known rate of vibration.

In order that the muscle-nerve preparation may not be injured by the tissues becoming too dry, it is placed in a small glass box, the air of which is kept moist by a damp sponge. This *moist chamber* is used when any living tissue is to be protected from drying.

The first myograph used was a complicated instrument devised by Helmholtz ; in which a small glass cylinder is made to rotate rapidly by a heavy weight, and when a certain velocity of rotation is attained, a tooth is thrown out by centrifugal force, which breaks the circuit of the current passing through the nerve of the muscle. The tendon is attached to a balanced lever, at one end of which hangs a rigid style pressed by its own weight against the glass cylinder. When the circuit is broken the muscle contracts, raises the lever, and makes the style draw on the smoked glass cylinder.

Fick introduced a flat recording surface moving by the swing of a pendulum, by which the abscissa is made a segment of a circle, and not a straight line, and the rate varies, so that the different parts of the curve have varying time-values. The curves given in the following wood-cuts are drawn with the *Pendulum Myograph.*

Du Bois-Reymond draws muscle curves on the smoked surface of a small glass plate contained in a frame, which is shot by the force of a

spiral spring along tense wires, and on its way breaks the contact. The trigger used for releasing the spring sets a tuning fork at the same time vibrating (*Spring Myograph*).

Single Contraction.

In response to an instantaneous stimulus, such as occurs in the secondary coil on breaking the primary current, a muscle gives a momentary twitch or spasm, commonly spoken of as a *single contraction*, which is of so short duration, that without the graphic method

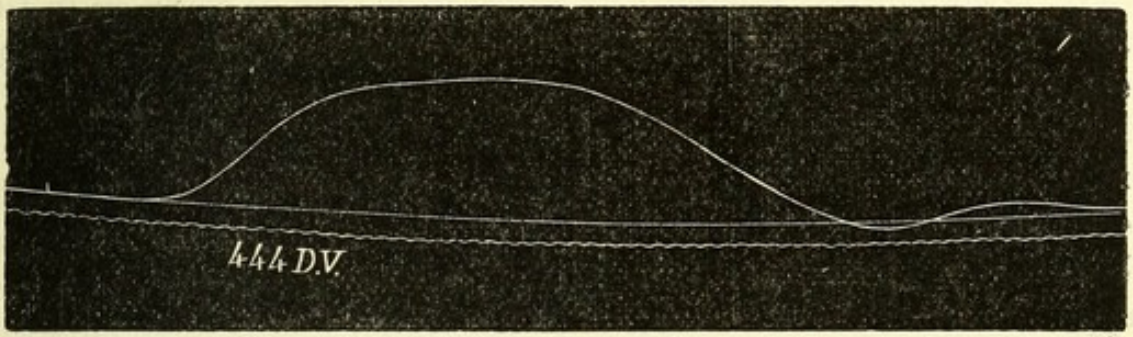


Fig. 185.—Curve drawn by a frog's gastrocnemius on the Pendulum Myograph; below is seen the tuning-fork record of the time occupied by the contraction. Parallel to the latter is the abscissa. The little vertical mark at the left shows the moment of stimulation, and the distance from this to the beginning of the rise of the curve gives the latent period, which is followed by the ascent and descent of the lever.

of recording the motion we could not appreciate the phases which are seen in the curve.

The curve drawn on the recording surface of a pendulum myograph, by such a single contraction, is represented in Figure 185. The short vertical stroke on the abscissa, or base line, is drawn by touching the lever when the muscle is in the uncontracted state, and indicates the time of stimulation. The upper curved line is drawn by the lever during the contraction of the muscle.

In such a curve the following stages are to be distinguished :—

1. A short period between the moment of stimulation and that at which the lever begins to rise, during which the muscle does not move. This is known as the *latent period*. In the skeletal muscles of the frog this period lasts nearly ·01 sec.

2. A period during which the lever rises, at first slowly, then more quickly, then again slowly, until it ceases to rise. This stage has been called the period of *rising energy*. It lasts about ·04 sec.

3. When the highest point is attained the lever commences to fall, at first slowly, then more quickly, and at last slowly. There is then no pause at the height of contraction. The stage of relaxing has been

called the period of *falling energy*. It occupies when quite fresh about the same time as the second period, viz., about ·04 sec.

Thus a stimulus occupying an almost immeasurably short time sets up a change in the molecular condition, which taking nearly $\frac{1}{10}$ sec. to run its course, and requiring $\frac{1}{100}$ sec. before it exhibits any change of form, then in $\frac{4}{100}$ sec. attains the maximum height of contraction, and without waiting in the contracted condition, spends $\frac{4}{100}$ sec. in relaxing.

The *latent period* which appears in a *single contraction curve* drawn by a muscle stimulated in the usual way, through the medium of a nerve, is not entirely occupied by *preparatory changes* going on in the substance of the muscle, but a certain part of the time recorded as latent period corresponds to the time required for the *transmission* of the impulse along the nerve. This may be shown by stimulating first the far end of the nerve and then the muscle itself. In this case two curves will be drawn having different latent periods, that obtained by direct stimulation of the muscle being shorter, and representing the real latent period, while the longer one includes the time taken by the impulse to travel along the piece of nerve between the electrodes and the muscle.

Wave of Contraction.—If one extremity of a long muscle be stimulated without the aid of the nerve (it is best to employ a muscle from a curarised animal), the contraction passes along the muscle from the point of stimulation in a wave which travels at a definite rate of 3—4 metres per sec. in a frog, and 4—5 metres per sec. in a mammal. Reduction of temperature and fading of vital activity cause the velocity of the wave to be lessened, until finally the tissue ceases to conduct; then only a local contraction occurs, severe stimulus causing simply an elevation at the point of contact. This seems analogous to the idio-muscular contraction, which marks the seat of severe mechanical stimulation after the general contraction has ended.

Variations in the Phases of a single Contraction.

The *latent period* varies much in different kinds of muscle, in the same kind of muscle of different animals, and in the same individual muscle under different conditions. As a rule the slow-contracting muscles have a longer latent period. Thus the non-striated slow-contracting muscles found in the hollow viscera have a latent period of some seconds. The striated muscles of cold-blooded animals have a longer latency than the same kind of muscle in birds and mammalia.

The same gastrocnemius of a frog has a shorter latent period when strongly stimulated, or when its temperature is raised, and *vice versâ*.

The latent period is considerably lengthened by fatigue. If the weight be so applied that it does not extend the muscle before contraction, but only bears on it the instant it commences to shorten, the duration of the latent period increases in proportion to the weight the muscle has to lift.

The *duration* of the single contraction of striated muscle varies in different cases and under varying circumstances. With submaximal

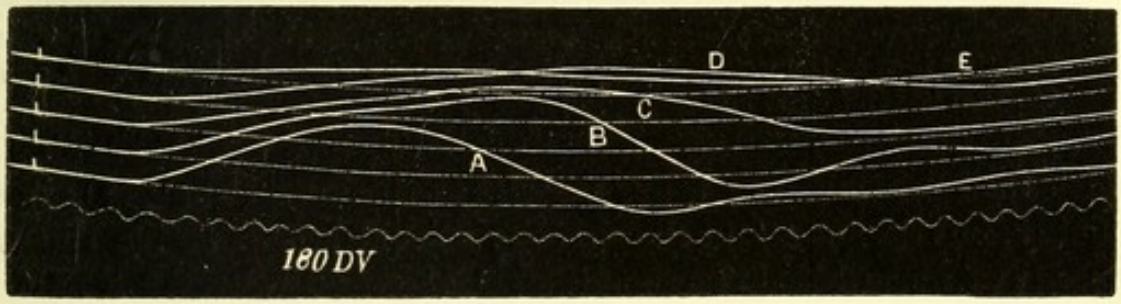


Fig. 186.—Curves drawn by the same muscle in different stages of fatigue—A, when fresh; B, C, D, E, each immediately after the muscle had contracted 200 times. Showing that fatigue causes a low, long contraction.

stimulation the length of the curve increases with the strength of the stimulation. When the maximal strength of stimulus (*i.e.*, that exciting a *maximal contraction*) is reached, no further lengthening of the curve takes place.

The greatest difference is observed in the muscles found in different kinds of animals. The contraction of some kinds of muscle tissue (non-striated muscle of mollusca, for example) occupies several minutes, and reminds one of the slow movement of protoplasm; while the rapid action of the muscle of the wing of a horsefly occurs 330 times a second. Various gradations between these extremes in the rapidity of muscle contraction may be found in the contractile tissues of different animals. The following table gives the rate of contraction of some insects' muscles, which may help to show the extent of these variations.

Horsefly . . .	330	contractions per second.
Bee	190	" "
Wasp . . .	110	" "
Dragon-fly . . .	28	" "
Butterfly . .	9	" "

Among the vertebrata the duration of the contraction of the skeletal muscles varies considerably according to the habits of the animal. The limb muscles of the tortoise and toad take a very long time to

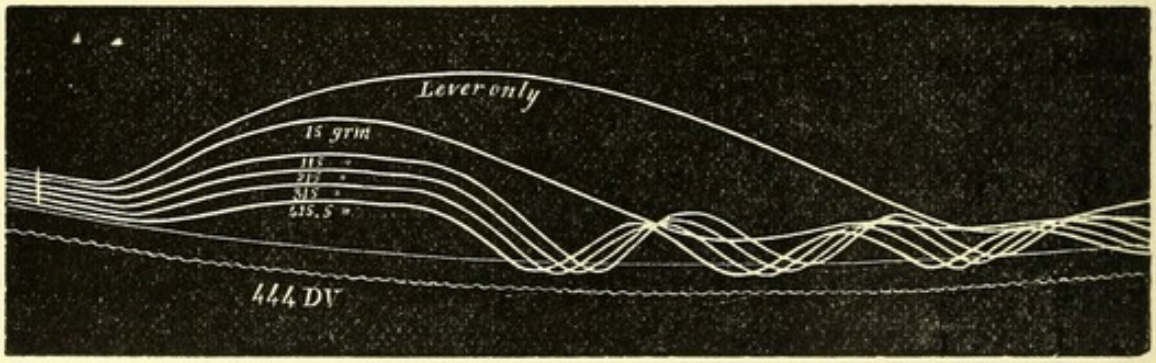


Fig. 187.—Six curves drawn by the same muscle when stretched by different weights. Showing that as the weight is increased the latency becomes longer and the contraction less in height and duration.

finish their contraction ; other muscles of the same animals act more quickly, but do not attain the rapidity of contraction of the skeletal muscles of warm-blooded animals.

The duration of a single contraction of the same muscle is also

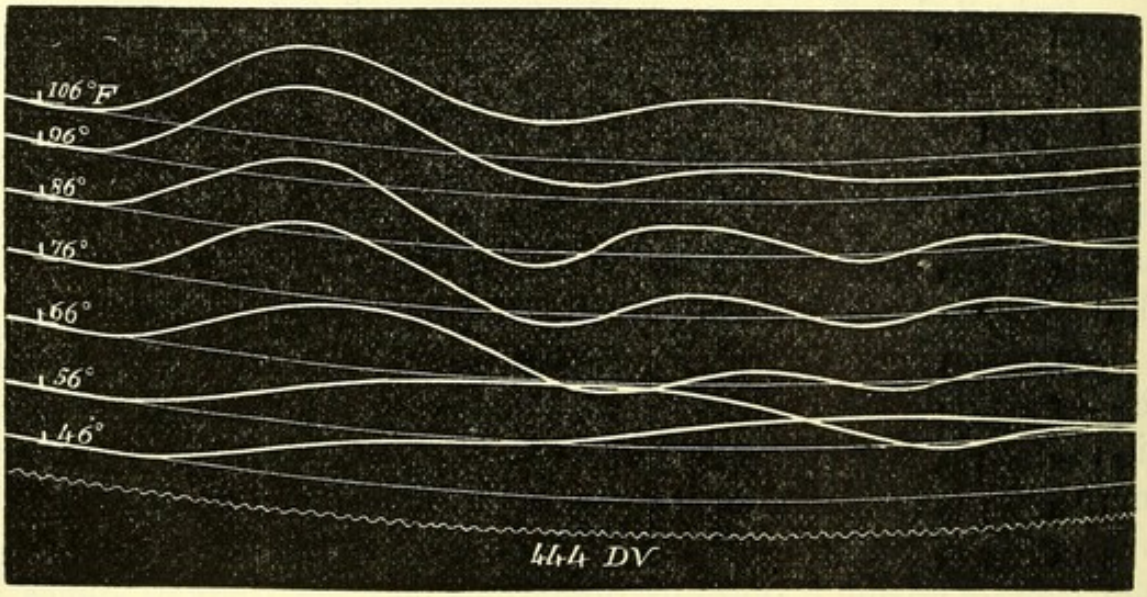


Fig. 188.—Curves drawn by the same muscle at different temperatures. Showing that with elevation of temperature the latency and the contraction becomes shorter. (The muscle had been previously cooled.)

capable of considerable variation. It seems to be lengthened by anything that leads to an accumulation of the chemical products which arise from muscle activity. Hence fatigue or over-stimulation cause a slow contraction (Fig. 186).

Moderate increase of temperature greatly shortens the time occupied by the single contraction of any given muscle. Excessive heat causes a state of continued contraction.

The reduction of temperature causes a muscle to contract more slowly, and, when extreme, the muscle remains contracted long after the stimulus is removed.

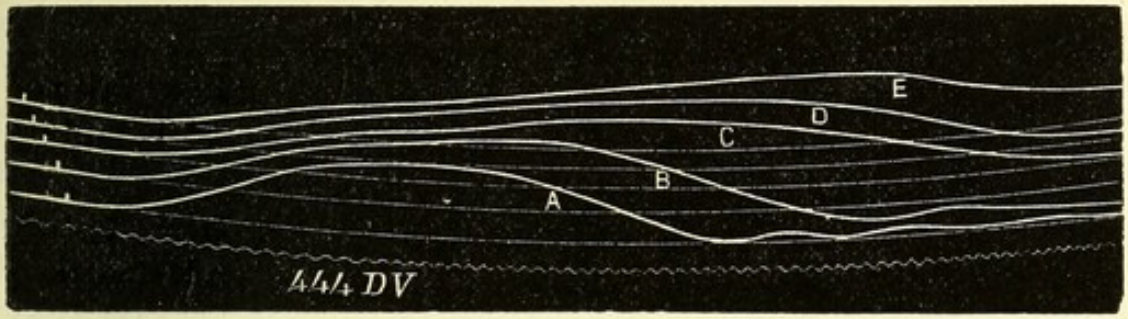


Fig. 189.—Curves drawn by the same muscle while being cooled. Showing that the latency and the contraction become longer as the temperature is reduced.

The *altitude* of the curve which represents the extent of the contraction varies in the same way as the latent period and the duration.

Maximum Contraction.

The extent to which a muscle will contract depends upon the conditions in which it is placed, and varies with the load, its

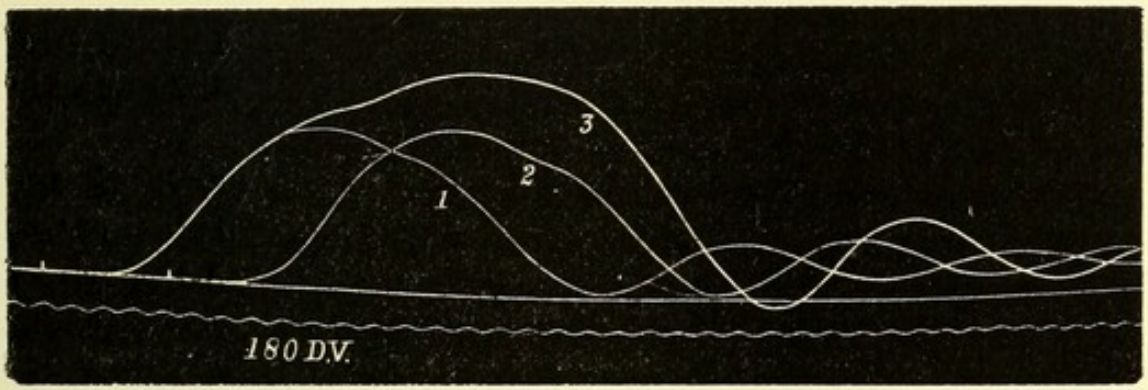


Fig. 190.—Pendulum Myograph tracings showing summation.

1. Curve of maximum contraction drawn by first stimulus, the exact time of application of which is shown by the small up-stroke of the left hand of the base line.
2. Maximum contraction resulting from second simple stimulation given at the moment indicated by the other small up-stroke.
3. Curve drawn as the result of double stimulation sent in at an interval indicated by the distance between the up-strokes, showing summation of stimulus and consequent increase in contraction over the "maximum contraction."

irritability, the temperature, and the force of the stimulus. A fresh muscle at the ordinary temperature with a medium load, will contract more and more as the intensity of the current employed increases.

There is a limit to this increase, and with comparatively weak stimulation an effect is produced which cannot be surpassed by the same muscle with further increment of stimulus. The height of the contraction is the same for all medium stimuli while the muscle is fresh. This is called the *maximum contraction*, being the greatest shortening which can be produced by a single stimulus.

Summation.—Each time a muscle receives an induction shock of medium strength it responds with a "maximal contraction," but this is not the maximum amount the muscle can contract with *repeated stimulation.* If a second stimulus be given while the muscle is in the contracted state, a new maximum contraction is added to the contraction already arrived at by the muscle at the moment of the second stimulation. If stimulated when the lever is at the apex of the curve the sum of the effect produced will be equal to two maximum contractions.

If applied in the middle of the period of the ascent or descent of the lever a second stimulation gives rise to $1\frac{1}{2}$ maximum contractions, and so on, in various parts of the curve, a new maximum curve is produced, arising from the point at which the lever is when the second stimulus is applied (Fig. 190).

During the latent period a second stimulation produces the same effect, but the summation only begins at the end of the latent period of the second contraction, when the effect of the first stimulus is as yet small. It is difficult to demonstrate the summation when the stimuli are very close, but if the second stimulus come after an interval of more than $\frac{1}{600}$ sec., summation can easily be appreciated.

This summation of effect also takes place when the stimulus is insufficient to produce a maximum contraction. The first few weak stimuli give rise to the same extent of contraction as if the muscle were at its normal length at the time of each successive stimulation. The following tracings (Figs. 191—193) show the effects of repeated stimulations applied at the various periods indicated by the numbers on the abscissa line.

Tetanus.

If a series of stimuli be applied in succession, at intervals less than the duration of a single contraction, a summation of contractions occurs, which results in the accumulation of effect until the muscle has shortened to about one-half of the length it attains during a single contraction, or about one-fourth the normal length of the relaxed muscle; it then remains contracted to the same extent for some time, and does not shorten further though the stimulus be

increased in rate or strength. As long as the stimuli are continued, the various single contractions caused by the individual shocks are fused together (Fig. 191); but if the intervals between the stimuli be nearly as long as the time occupied by a single contraction, the line

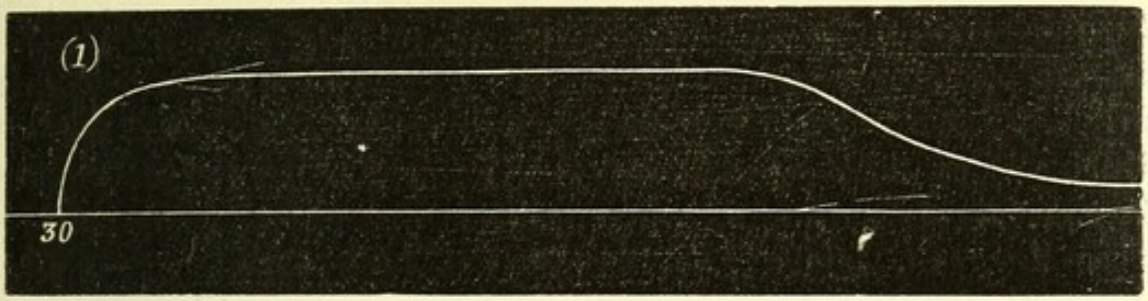


Fig. 191.—Curve of tetanus resulting from 30 stimulations per second, drawn by a frog's muscle on a drum, the surface of which moves 1·5 centimeter per second. The stimulation commences at "30," and ceases just before the lever begins to fall. No trace of the individual contractions of which the tetanus is composed can be recognised.

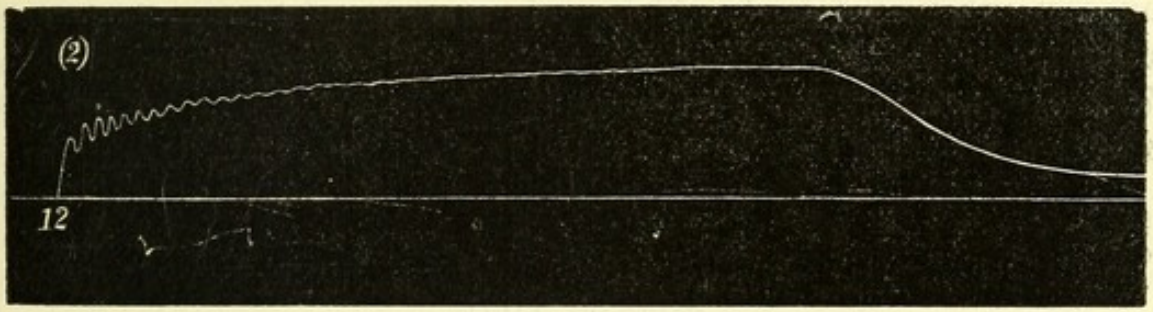


Fig. 192.—Curve of tetanus composed of imperfectly fused contractions resulting from 12 stimulations per second. The serrations on the left of the curve indicate the individual contractions.

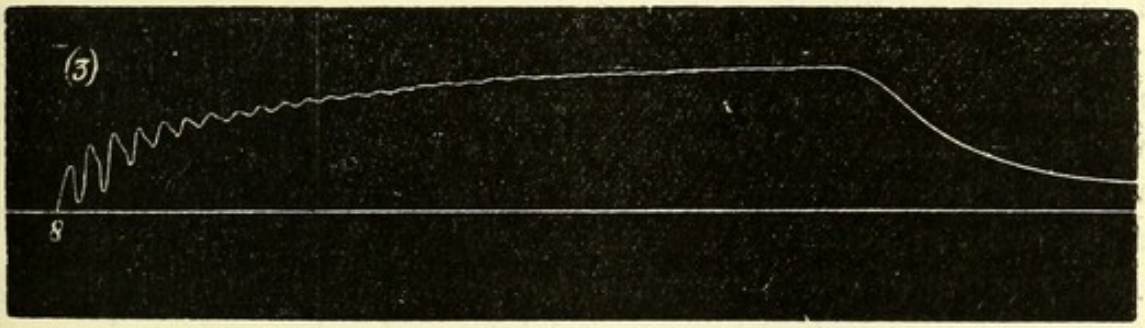


Fig. 193.—Tetanus produced by 8 stimulations per second. The more perfect fusion of the single contractions shown towards the end of the curve depends on the altered condition of the muscle.

drawn by the lever will show notches indicating the apices of the fused single contractions (Figs. 192 and 193).

This condition of summation of contractions is called *tetanus*, and is said by some to be the manner in which muscular motion is produced by the action of the nerves in obedience to the will.

With from fifteen a second to upwards of many hundreds of induced shocks one can produce tetanus in a frog's muscle. The lowest rate of electric stimulation at which human muscle passes into complete tetanus is about 25 per sec. The number of stimuli required varies with the rate of contraction of the muscle employed, the quick contracting bird's muscle requiring 70 per second, while the exceptionally slow-moving tortoise muscle only requires 3 per second. According to some, there is a limit to the number of stimuli which will cause tetanus, 360 per second is named as the maximum for a certain strength of stimulus; with stronger stimuli, even when more frequent, tetanus occurs. It has been shown that many thousand stimuli per second can cause tetanus even with very weak currents. If tetanus be kept up for some seconds, and the stimulation be then suddenly stopped, the lever falls rapidly for a certain distance, but the muscle does not quite return to its normal length for some few seconds. This residual contraction is easily overcome by any substantial load. If kept in a state of tetanus by weak stimulation, after some time the muscle commences to relax from fatigue, at first rapidly, then more slowly. This falling off of the tetanic contraction may be prevented by increasing the stimulus.

Muscle Tone.

Although the tracing drawn by a lever attached to a muscle in tetanus is straight, and does not show any variation in the tension of the tetanised muscle, some variations in tension must occur, since a low humming sound is produced during contraction. A *muscle-tone*, like the purring of a cat, can be heard by applying the ear firmly over any large muscle (biceps) while in tetanus, by throwing the muscles attached to the orbit and Eustachian tube into powerful action, or by spasm of the muscles in mastication.

The number of vibrations which has been estimated to occur in the voluntary contraction of human skeletal muscles does not produce an audible note; hence it has been supposed that the note we hear is an overtone. When a muscle is thrown into tetanus by a current interrupted by a tuning fork, a tone is produced which corresponds with that of the fork causing the interruption in the current by definite vibrations, which regulate the number of stimulations the muscle receives. If, on the other hand, a contraction of the muscle be brought about by stimulating the spinal cord, with the same rate of breaking the current, the normal muscle-tone is

produced, as if the contraction were the result of a nerve impulse coming from the brain.

There is no satisfactory proof, however, that the variation in tension of the continuous contraction of voluntary muscle is strictly rhythmical. The sensation of a sound like the muscle-tone is produced by any *nearly* periodic vibrations of less rate than 25 per sec. The pitch of the muscle-tone varies with the tension of the membrana tympani. Hence it has been suggested that it corresponds with the resonant tone proper to the membrane of the drum; which may be evoked by any trembling movements of the muscle fibres due to slight variations in the force or distribution of the impulses transmitted by the motor nerves.

Irritability and Fatigue.

The activity of the muscle tissue of mammalian animals is closely dependent upon a good supply of nutrition, and if its blood current be completely cut off by any means for a length of time it loses its power of contracting. While the muscle remains in the body, and is kept warm and moist by the juices in the tissues, it will live a very considerable time without any blood flowing through it, and it at once regains its contractility when the blood stream is again allowed to flow through its vessels. This is seen when the circulation of a limb is brought to a standstill by means of a tourniquet or a tightly applied bandage. A mammalian muscle soon ceases to be irritable and dies when removed from the body, but its functional activity may be renewed by passing an artificial stream of arterial blood through its vessels, and an isolated muscle may thus be made to contract repeatedly for a considerable time.

On the other hand, the muscle of a cold-blooded animal will remain alive for a long time—many hours—if kept cool and moist. When its functional activity is about to fade, it may be revived by means of an artificial stream of blood caused to flow through its vessels, just as in the case of the mammalian muscle.

Common experience teaches us that even when well supplied with blood our muscles become fatigued after very prolonged exertion, and are incapable of further action. This occurs all the more rapidly when anything interferes with the flow of blood through them, such as using our arms in an elevated position: the simple operation of driving in a screw overhead is soon followed by pain and fatigue in the muscles of the forearm, though the same amount of force could

be exerted when the arms are in a lower posture without the least feeling of fatigue.

The difficulties of experimenting with the muscles of mammals make the frog-muscle the common material for investigation, and from it we learn the following facts :—

1. When removed from the body and deprived of its blood supply, the muscle of a cold-blooded animal slowly dies from want of nutrition. If it be placed under favourable circumstances, and allowed perfect rest, it may live twenty-four hours. If it be frequently excited to action, on the other hand, it rapidly loses its irritability, being worn out by fatigue.

2. From a muscle removed from a recently killed animal, we learn, that even without a supply of blood the muscle-tissue is capable of recovering from very well-marked fatigue, if it be allowed to rest for a little time, so that the muscle has in itself the material requisite for its recuperation.

The first question then is, what causes the loss of irritability which we call fatigue? And the second is, by what means is the muscle enabled to return to a state of functional activity? We know that the mere life of a tissue must be accompanied by certain chemical changes which require (*a*) a supply of fresh material, and (*b*) the removal of certain substances which are the outcome of the tissue-change.

In the case of muscle this chemical interchange is constantly but slowly going on between the contractile substance and the blood. When the muscle contracts, much more active and probably different changes go on in the contractile substance, more new material being required, and more effete matter being produced. It is probable that the accumulation of these effete matters is the more important cause of the loss of irritability in a muscle, for a frog's muscle when quite fatigued may be rendered active again by washing out its blood vessels with a stream of salt solution of the same density as the serum (·6 per cent. NaCl), and thus removing the injurious "fatigue-stuffs," as they have been called. It is found that a very minute quantity of lactic acid injected into the vessels of a muscle destroys its irritability, and brings it to a state resembling intense fatigue. Of the new materials required for the sustentation of muscle irritability, oxygen is amongst the most important, though its supply is not absolutely necessary for the recuperation of a partially exhausted, isolated frog's muscle.

The slow recovery of a bloodless muscle from fatigue may be explained by supposing time to be necessary for the reconstruction of

new contractile material, and probably also for a secondary change to take place in the effete materials by which they become less injurious.

When working actively the muscles require an adequate supply of good arterial blood in order to ward off exhaustion; and, as already explained in speaking of the vasomotor influences, a muscle receives a greater supply of blood when actively contracting than when in the passive state.

The irritability of a muscle and the rate at which it becomes exhausted may be said to depend upon :—

1. The adequacy of its blood supply: the better the supply of new material and the more quickly the injurious effete materials are removed, the more work a muscle can do without becoming exhausted.

2. Temperature has a marked effect on the irritability of muscles as well as upon the form of this contraction. Low temperatures—approaching 5° C.—diminish the irritability of a muscle, but do not seem to tend towards more rapid exhaustion. High temperatures —approaching 30° C.—increase the irritability, and at the same time rapidly bring about fatigue. At about 35° C. an isolated frog's muscle begins to pass into heat tetanus, and permanently loses its irritability.

3. Functional activity is accompanied by an increased blood-supply, and a more perfect nutrition of the muscles, hence activity is advantageous for their growth and power; while, on the other hand, continued and prolonged inactivity causes a lowering of the nutrition and loss of irritability. Thus when the nerves supplying the voluntary muscles are injured, there is considerable danger of atrophy and tissue-degeneration of the muscles; the contractile substance becomes replaced by fat granules. This degeneration also occurs in the stump when a limb is amputated, the distal attachments of the muscles having been cut they cannot act, and after some time they become completely atrophied, so that muscle tissue can hardly be recognised in them.

Death Rigor.

The death of muscle tissue is associated with a set of changes which, in some respects, resemble those observed in its active state. The most obvious phenomenon is an unyielding contraction, which causes the stiffening of the body after death. Hence it is called *rigor mortis*. The muscles harden; lose their elasticity, and the

tissue is *torn* if forcibly stretched. When isolated, the muscle is seen to be opaque, and its reaction is found to be distinctly acid. A considerable quantity of heat is developed during the progress of the rigor. The electric currents alter in direction and finally disappear.

The period at which rigor comes on and its duration depend on (*a*) the state of the muscles, and (*b*) the circumstances under which they are placed at the time of death. All influences which tend to cause death of the tissue induce early rigor of short duration, viz., (1.) Prolonged activity—as may be shown in a muscle artificially tetanised, or seen in an animal whose death was preceded by intense muscular exertion—causes rigor to appear almost immediately, and to terminate rapidly. (2.) High temperature facilitates the production of rigor in dying muscles, indeed a temperature not much exceeding that normal to the tissue induces rigor. This form of contraction, which is called *heat-rigor*, is brought about in mammalian muscles by a temperature of about 50° C., and in frogs' muscles below 40° C. If, however, the temperature of a muscle be suddenly raised to the boiling point, it is killed, and the chief phenomena of rigor are prevented from occurring. (3.) Freezing postpones the changes in the muscles upon which rigor depends. (4.) Stretching, or any mechanical excitation which tends to injure the tissue, causes it to pass more rapidly into rigor. (5.) The application of water and of a number of chemical substances cause muscles quickly to pass into a state of rigor similar to that which ordinarily follows the death of the tissue. (6.) Any stoppage in the blood-current normally flowing through a muscle, after some time makes it pass into a state of rigidity like rigor mortis, but this may be removed by allowing the blood to flow freely again through the muscle.

It is generally admitted that rigor mortis depends on the tendency of the muscle plasma to coagulate and give rise to myosin and muscle serum. This is in most respects comparable with the coagulation of the blood, and may also depend upon the action of some ferment, of which there is no lack in dead muscle tissue. Compare the paragraph on chemistry, p. 378.

Most of the phenomena of the process of muscle-rigor remind us of the changes already described as occurring in muscle, when it passes from the passive to the active state. Thus the shortening of the fibres, the evolution of heat, and the chemical changes may be said to be identical in contraction and rigor mortis. The electrical changes are, however, very transitory, and the rigor is accompanied by complete loss of elasticity and irritability. Opacity of the tissue marks its later stages.

Thus, while dying, the muscle tissue may be said to go through a series of events analogous to those which would occur in a prolonged contraction without any period of recuperation. The idea naturally has suggested itself to the minds of physiologists that the active state of muscle depends upon chemical changes which are the initial steps in the coagulation of the contractile substance, when the muscle is dying. The muscle tissue is supposed to contain a special proteid of extremely intricate and unstable chemical constitution, which is constantly undergoing slow molecular change, and which if not re-integrated by constant assimilation would pass into coagulation. Under the influence of stimuli a comparatively sudden and intense molecular disturbance is brought about, which produces shortening of the fibres and the same chemical changes as precede the coagulation. Before the stage of coagulation appears a chemical re-arrangement takes place, the result of which is the re-construction of the unstable complex proteid. If nutriment be withheld, or if the stimulation be too powerful, the recovery cannot take place, and we find the muscle passing from a state of physiological contraction to one of intense exhaustion, and then to coagulation and death.

UNSTRIATED MUSCLE.

So far reference has only been made to the skeletal muscles, the fibres of which are marked by transverse striations, and whose single contraction is extremely rapid and short. The contractile tissues which carry on the movements in the various organs of the body are not striated fibres, but, as has been already stated, consist of elongated flattened cells with rod-shaped nuclei. They occur generally in the form of sheets or layers, forming coats for the organs in which they lie. Their single contraction is slow and prolonged, and is generally transmitted from one muscle-cell to another as a kind of sluggish wave. They are not capable of passing into a tetanic state of contraction like striated muscles.

The slowest contraction seems to be that of the muscle-cells in the walls of the blood-vessels. These remain in a state of partial contraction, which undergoes a brief and temporary rhythmical relaxation. The most forcible aggregate of unstriated muscle elements is met with in the uterus. This organ, which has very exceptional

motor powers to perform, contracts in somewhat the same way as the muscles of the blood-vessels, but more quickly, and with longer rhythmical intervals of partial relaxation. The muscular wall of the intestine and the iris are among the most rapidly contracting smooth muscles.

The chemical properties of the smooth muscle are somewhat similar to those of striated skeletal muscles, and they pass into a state of rigor, while dying, which seems to depend on the same causes as the rigor mortis already described.

CHAPTER XXVI.

THE APPLICATION OF SKELETAL MUSCLES.

THE consideration of the many varieties of muscles, and the various modes in which they are attached to the bones that they are destined to move, belongs to the department of practical anatomy, and needs no mention here. As a general, but by no means universal rule, a muscle has one attachment which is fixed, commonly spoken of as its *origin*, and a second, called its *insertion*, upon which it acts by approximating it to the origin. Muscles usually pass in a straight line between their two attachments, but sometimes they act round an angle by sliding over a pulley, or by means of a small bone in the tendon, like the patella.

The muscles are so attached that they are always slightly on the stretch, and thus at the moment they begin to contract they are in an advantageous position to bring their action to bear on the bones which they move. When the contraction ceases the bones are drawn back to their former position without any sudden jerk or jar.

The muscles act upon the bones as levers by working upon the short arm of the lever, so that more direct force is required on the part of a muscle than the weight of the body moved; but from this arrangement considerable advantages are gained, viz., that a small contraction of the muscle causes an extensive excursion of the part moved, and much greater rapidity of motion is attained.

All the three orders of levers are met with in the movements of the different bones of the skeleton; often, indeed, all three varieties are found in the same joint, as the elbow, where the simple extension and flexion motions of the biceps and triceps muscles give us good examples (Fig. 194).

The *first* order of lever is used when the triceps is the power and draws upon the olecranon, thus moving the hand and forearm around the trochlea which acts as the fulcrum. This is shown in the upper diagram, in which the hand is striking a blow with a dagger.

The *second* order comes into play when the hand, resting on a

point of support, acts as the fulcrum, and the triceps pulling on the olecranon is the power which raises the humerus upon which is fixed the body or weight (middle diagram).

The *third* order may be exemplified by the action of the biceps in ordinary flexion of the elbow. Here the muscle, which is the power, is placed between the fulcrum—represented by the lower end of the humerus—and the weight which is carried by the hand (lower diagram).

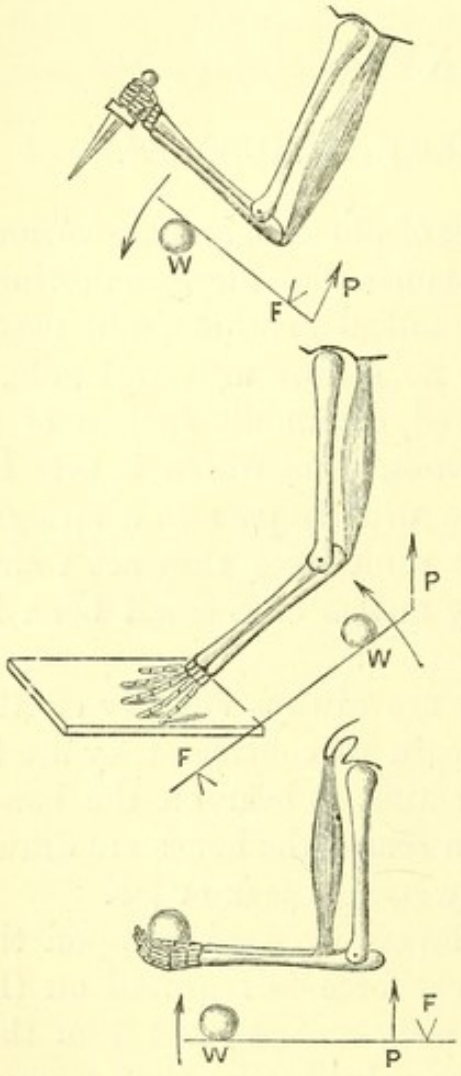


Fig. 194.—Diagrams showing the mode of action of the three orders of levers (numbered from above downwards) illustrated by the action of the elbow joint.

The various groups of muscles which are so arranged as to assist each other when acting together, are called *synergetic*, and those which when contracting at the same time oppose each other, are called *antagonistic*. The same muscles may, in different positions of a joint or in combination with other muscles, have totally different actions, at one time being synergetic and at another antagonistic. Thus, the sterno-mastoid muscle may, in different positions of the head, either bend the cranium backwards or forwards, and so co-operate with two sets of muscles which are definitely antagonistic to one another.

Joints.

The unions between the bones of the skeleton are very varied in function and character. They may be classified as:—

1. Sutures, in which the bones are firmly united by rugged surfaces without the interposition of any cartilage. They are practically only the lines of union of different bones, which grow together to form a single bone.

2. Symphyses, in which two bony substances are strongly cemented together by ligaments, and a more or less thick adherent layer of fibro-cartilage, are joints allowing of some movement, which is, however, very limited.

3. Arthroses, or true movable joints, such as are commonly met

with in the extremities. They are characterised by a synovial sac lining the surrounding ligaments, and two smooth surfaces of cartilage which cover over the bony extremities taking part in the articulation, and form what are called the articular surfaces. The synovial sac is strengthened by a loose membranous covering—the capsular ligament—which is attached round the edge of the cartilages next to the periosteum, which here ceases.

The articular surfaces are always in exact and close contact, being pressed together by the following influences :—(1.) The elastic tension and tonic contraction of the surrounding muscles, which exert considerable traction on them. (2.) The traction of the surrounding ligaments, which in some cases holds the bones firmly together, no matter what their relative positions may be. This can be well seen in the knee-joint, in which a comparatively small number of the ligaments suffice to keep the articular surfaces in contact. (3.) The atmospheric pressure also tends to hold the bones in close apposition, as may be seen in the hip-joint, which is not easily disarticulated, even when all the surrounding structures and the ligaments have been severed.

The synovial joints may be classified according to the form of their surfaces, or their mode of motion as follows :—

1. Flat articular surfaces held together by a short rigid capsule allowing of but very slight gliding movement ; examples of this form of joint are to be found in the tarsus and the articular processes of the vertebræ.

2. Hinge joints, in which the surfaces are so adapted that only one kind of motion can take place. A groove-like cavity in one bone fits closely and glides around the axis of a roller on the other bone, while the sides of the joint are kept tightly together by means of strong lateral ligaments. Examples of this form of joint are to be found between the phalanges of the digits and at the humero-ulnar joint.

3. The rotatory hinge, or pivot joint, in which a part moves round the axis of a bone, instead of the axis of rotation being at right angles to both bones, forming the joint as in an ordinary hinge. Such joints are seen at the head of the radius and at the articulation between the atlas and the adontoid process of the axis.

4. A saddle-shaped joint is a kind of double hinge, in which each of the articulating bones forms a partial socket and roller, and hence there are two axes of rotation placed more or less at right angles one to the other. A good example of this kind of joint occurs between the thumb and one of the wrist bones.

5. Spiral articulations are modifications of the hinge, in which the surface of the roller does not run "true," but becomes eccentric, so that the surface of the roller forms really part of a spiral by means of which the bone articulating with it is forced away from the central axis of rotation and becomes jammed as if stopped by a wedge. The best example of this is the knee. In this joint the axis of rotation (C) is near the posterior surfaces of the bones, and passes transversely through the condyles of the femur, the surfaces of which form an arc, the centre corresponding to the axis of motion. In ordinary flexion the head of the tibia (F) moves on the arc around the axis so as to partially relax the lateral ligament and allow of some rotation on the axis of the tibia. When the head of the tibia moves forwards, in extension (E), it becomes wedged against the anterior part of the articular surface of the femur (W), which presents an eccentric spiral-like curve, departing more and more from the centre of rotation as the articular surface of the tibia proceeds forwards. The effect of this is, that in extension of the leg the ligaments are made tense, and the bones are firmly locked together. Owing to the inequality between the size of the internal and external condyles the axis of rotation is not at right angles to the axis of the femur, but is at such an angle that extreme extension causes a slight amount of outward motion of the leg.

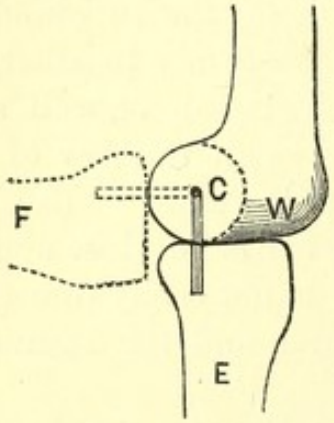


Fig. 195.—Diagram of the action of the knee-joint.

W = articular surface of femur.
E = tibia in position of extension.
F = tibia in position of flexion.
C = centre of rotation.

6. In the ball and socket joints—the name of which implies their mechanism—the most varied movements occur. (Hip and shoulder.)

Standing.

In order that an elongated rigid body may stand upright it is only necessary that a line drawn vertically through its centre of gravity should pass within its basis of support, and if the latter be sufficiently wide the object will remain permanently in that position. The human body, in the first place, is not rigid, and in the second place the basis of support is too small to ensure a satisfactory degree of steadiness. The act of standing must, therefore, be accomplished by the action of certain muscles, which are employed in

preventing the different joints from bending, and in so balancing the various parts of the body as to keep the whole frame from toppling over.

In order to economise muscular energy while standing, we may lock the more important joints, and thus depend rather on the passive ligaments than upon muscular action for the rigidity of the body. With this object we are taught to place the heels together, turn out the toes, bring the legs parallel by approximating them, and extending the knees to the utmost, to straighten and to throw back the trunk so as to render tense the anterior hip ligaments, to direct the face straight forwards so as to balance the head evenly, and to let the arms fall by the sides.

In this position, as a soldier stands at attention, the knee and hip joints remain fixed, without any effort on the part of the muscles, but it is far from being the most comfortable attitude one can assume for prolonged standing, and hence the position known best by the order "stand at ease" is adopted if more complete rest is desired. In this position the weight of the body is usually allowed to rest on one leg while the other lightly touches the ground to form a kind of stay and relieve the muscles which surround the supporting ankle from too great an effort of balancing. At the same time the knee is extended and the pelvis becomes somewhat oblique so as to bring it more directly over the head of the femur. In ordinary easy standing, the joints are not usually kept locked by the tension of the ligamentous structures, but their position is constantly being very slightly altered so as to vary the muscles employed in preserving the balance and thus prevent fatigue.

The joints most exercised in the erect posture are the following:—

1. The *ankle* has to support the weight of the entire body, while the joint is neither flexed nor extended to its utmost, and cannot be fixed in this position by ligamentous arrangements. The foot being placed on the ground, resting on the heel and the balls of the great and little toes, is supported in an arch-like form by strong though elastic ligaments, which allow but little motion in the numerous joints. The bones of the leg can move in the freest way, backwards or forwards, over the articular surface of the astragalus, which forms the roller of the hinge, lateral motion being prevented by the malleoli. The line passing through the centre of gravity of the body generally falls slightly in front of the axis of rotation of the ankle-joint, so that the entire body tends to fall forwards at the ankles. This tendency is checked by the powerful calf muscles, which, attached to the calcaneum by means of the strong tendo

Achillis, keep the parts in such a position that an exact balance is almost constantly kept up.

2. The *knee-joint*, when completely extended, requires no muscular action to prevent it from bending, because the line of gravity then passes in front of the axis of rotation, and the weight of the body tends to bend the knee backwards. This is impossible on account of the strong ligaments which exert their traction behind the axis of rotation. As a rule, these ligaments are not put on the stretch in this way, but the joint is held, by muscular power, in such a position that the line of gravity passes just through, or very slightly behind, the axis of rotation of the joint, so that, if anything, there is a slight tendency for the knee to bend. This is completely checked, and the body balanced by the powerful extensor muscles of the thigh.

3. In the *hip joints*, which have to support the trunk and head, the line of gravity falls just behind the line uniting the joints when the person is perfectly erect, so that here the body has a tendency to fall backwards. This is prevented by the strong ilio-femoral ligament. When, however, the knee is not straightened to the full extent, so that the line of gravity passes through or a little behind the axis of rotation of that joint, then the pelvis is very slightly flexed on the femora so that the axis of the joints lies exactly in or a little behind the line of gravity, and thus the body inclines rather to fall forwards. This tendency is prevented by the powerful glutei muscles, which also enable us to regain the erect posture after bending the trunk forwards.

The motions of which the *pelvis* and *vertebral column* are capable are too slight to deserve attention here. The vertebral column, wedged in as it is between the two innominate bones, may be taken, together with the pelvis, as forming a very yielding and elastic, but practically jointless, pillar, the upper part of which can alone be bent to such an extent as to require mention in discussing the mechanism of station.

The individual joints between *the cervical vertebræ* permit but a slight amount of movement when taken separately, but by their aggregate motion they enable considerable extension and flexion of the neck to take place. These motions follow so closely, and are so inseparably associated with those of the head on the upper vertebra, that there is no need to consider them separately from the latter.

The *atlanto-occipital joints* admit of some little lateral movement, but that in the antero-posterior direction is much the more important, but even this would be insignificant were it not associated with the movements between the other cervical vertebræ.

The cranium has then to be balanced on the top of a flexible column, and rests immediately in a kind of socket, which can move as a double hinge around two axes at right angles one to the other. The vertical line from the centre of gravity of the cranium must vary with every forward, backward, or lateral movement of the head or neck, but in the erect posture it passes a little in front of the axis of rotation of the atlanto-occipital joint and somewhat behind the curve of the cervical vertebræ, so that the head may be said to be poised on the apex of the vertebral column, with some tendency to fall forwards. There are no ligamentous structures which can lock the joints so as to keep the head in the erect position; therefore without the aid of muscular force the head will fall forwards or backwards according to the position it may be in when the muscles suddenly relax, as happens in falling asleep in the upright posture.

From the foregoing facts it will be seen that there exists a kind of co-ordinated antagonism at work in ordinary easy standing which keeps the elastic pliable body upright, without the rigidity adopted when standing "at attention." The muscular action is more exercised when we are not on steady ground and varied co-ordination becomes necessary; for instance, when we go on board ship for the first time. Standing then takes some little time to become easy, and requires new associations of movement. The gastrocnemius and soleus relax the ankle in a degree just proportionate to the amount of flexion of the knee permitted by the quadriceps extensor cruris, while simultaneously the great gluteal muscle allows the body to incline forwards so as to keep its centre of gravity in the proper relation to the basis of support.

Walking and Running.

Walking is accomplished by poising the weight on one foot and then tilting the body forwards with the other, which is then swung in front and placed on the ground to prevent falling. These acts are performed alternately by each leg, so that the "swinging limb" becomes the "supporting limb" of the next step. The swinging leg is described as having two phases, (1) active while pushing off from the ground, and (2) passive, while swinging forwards like a pendulum. In starting, one foot is placed behind the other, so that the line of gravity lies between the two, the hindmost limb having the ankle and knee a little bent. By suddenly straightening these joints it gives a "push off" with the toes and propels the body forward, so as to move it around the axis of motion of the fixed, or

supporting ankle-joint. At the end of the swing, the pendulous leg comes to the ground and leaves the other limb in the attitude ready for the push off. Thus on level ground walking is carried on with but small muscular exercise; but in ascending an incline or going up stairs, the supporting limb has to elevate the body at each step by extending the knee and ankle joints by the thigh extensors and the calf muscles.

Running is distinguished from walking by the fact that, while in the latter both feet rest on the ground for the greater part of each pace, in the former the time that either foot rests on the ground is reduced to a minimum, and the body can never be said to be balanced on either leg, so that in fact there is no longer a "support-limb." The legs are kept in a semi-flexed position ready for the push off or spring, which is so forcibly carried out that the body is propelled through the air without any support between each step, and has a constant tendency to fall forwards. Thus an interval, of greater or less duration according to the pace, exists during which both the feet are off the ground, because the moment either foot comes to the ground it at once executes a new spring without waiting for the swing of the other.

CHAPTER XXVII.

VOICE AND SPEECH.

THE human voice is produced by an expiratory blast of air being forced through the narrow opening at the top of the windpipe called the glottis. This glottis, which lies in the lower part of the larynx, is bounded on each side by the edges of thin, elastic, membranous folds that project into the air-passages. These membranous folds, called the vocal cords, are set vibrating by the current of air from below, and in turn communicate their vibrations to the air in the air-passages situated above them.

ANATOMICAL SKETCH.

The vocal apparatus produces sound in the same manner as a musical instrument of the reed-pipe variety. If we compare it with the pipe of an organ, we find all the parts of the latter represented. The lungs within the moving thorax act as the bellows. The bronchi and trachea are the supply pipes and air box. The vocal cords are the vibrating tongues; while the larynx, pharynx, mouth, and nose, act as the accessory or resonating pipes. The blast of air is produced and regulated by the respiratory muscles; and special intrinsic muscles of the larynx change the conditions of the vocal cords so as to alter the pitch of the notes produced. Other sets of muscles, by altering the conditions of the resonating pipes, give rise to many modifications in the vocal tones, and thus produce what is called *speech*.

The *larynx*, which may be regarded as the special organ of voice, is made up of four cartilages, viz., the cricoid, thyroid, and two arytenoids, jointed together so as to allow of considerable motion. Of these the inferior, the *cricoid*, is attached to the trachea which it joins to the others. It forms a ring, which is thin in front, but deep and thick behind, owing to a peculiar projection upward of its

posterior part. The *thyroid* consists of two side wings so bent as to form the greater part of the anterior and lateral boundaries of the voice box, and can be felt easily in the front of the throat. It is articulated to the sides of the cricoid by its two inferior and posterior extremities, so that the upper part of the cricoid cartilage can move backwards and forwards. The *arytenoid* cartilages are little three-sided pyramidal masses placed on the upper surface of the posterior part of the cricoid, to which they are attached by a loose joint. They are so placed that one surface looks inwards, the second backwards, and the third forwards and outwards, while the inferior surface rides on the cricoid. One point looks forwards, and to it is attached the vocal cord on each side, hence it has been called the vocal process. The apex, which looks outwards and backwards, gives attachment to some of the intrinsic muscles, and hence has been called the muscular process.

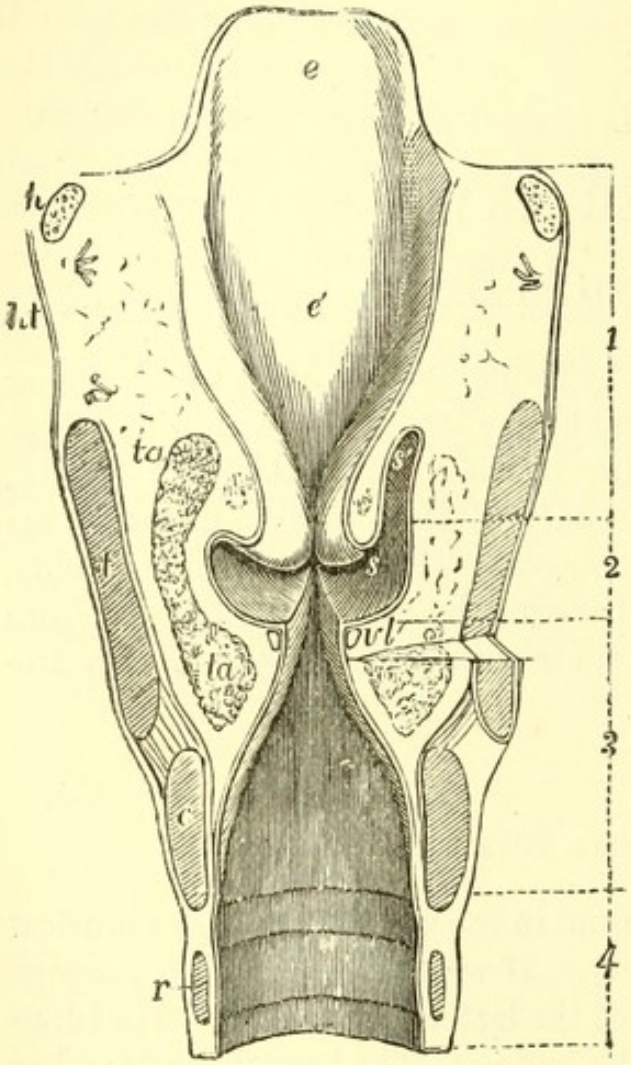


Fig. 196.—Anterior half of a transverse vertical section through the larynx near its middle, seen from behind. More is cut away on the upper part of the right side. 1. Upper division of the laryngeal cavity; 2. Central portion; 3. Lower portion continued into 4, trachea; *e*, epiglottis; *e'*, its cushion; *t*, thyroid cartilage seen in section. *vl*, true vocal cord at the rima glottidis; *s*, ventricle of larynx; *s'*, saccule. (A. Thomson.)

The thyroid cartilage is connected with the cricoid below, and with the hyoid bone above by ligaments and tough membranes, which hold the parts together, fill in the intervals, and complete the skeleton of the larynx.

The vocal cords are composed of small strands of elastic tissue, which are stretched between the anterior processes of the arytenoid cartilages and the inferior part of the thyroid, where they are attached side by side to the posterior surface of the angle formed by the junction of the two lateral parts or alæ of the thyroid. The mucous

membrane which lines the larynx is thin, and closely adherent over the vocal cords. The surface of the laryngeal cavity is smooth and even, the lining membrane passing over the cartilages and muscles so as to obliterate all ridges except the vocal cords and two others, less sharply defined, called the false vocal cords, which lie parallel to and above the true vibrating cords. Between these is the cavity known as the ventricle of the larynx.

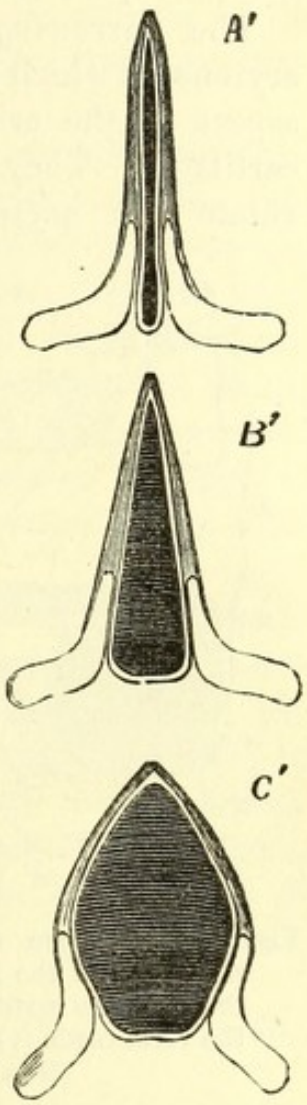


Fig. 197. — Diagrams taken from the laryngoscopic view of the larynx, showing in transverse section the position in which the vocal cords and the arytenoid cartilages are supposed to be during different actions of the larynx.

A'. Vocal chink as in singing.

B'. In easy quiet inhalation of air.

C'. In forced inspiration.

Mechanism of Vocalisation.

Shape of the opening of the glottis.—Taking the thyroid cartilage as the fixed base, the cricoid and arytenoid cartilages undergo movements which bring about two distinct sets of changes in the glottis and its elastic edges, namely, (1) widening and narrowing the opening; (2) stretching and relaxing of the vocal cords. During ordinary respiration the glottis remains about half open, being slightly widened during inspiration (B'). During forced inspiration the glottis is widely dilated by muscular action (C'). If an irritating gas be inspired, the glottis is tightly closed by a spasmodic action of certain muscles, so that the true vocal cords act as a kind of valve.

During vocalisation the glottis is formed into a narrow chink with parallel sides (A'), while the cords are made more or less tense, according to the pitch of the note to be produced; both these changes are brought about by muscular action.

The *opening* of the chink of the glottis is accomplished chiefly by a muscle called the posterior crico-arytenoid, which passes from the posterior surface of the cricoid cartilage to the outer and posterior angle of the arytenoids. By pulling the latter point downwards and backwards it separates the arytenoid cartilages, particularly at their anterior extremity, where the cords are attached. In this action it is aided by a small muscle connecting the posterior surfaces of the arytenoid, namely, the posterior arytenoid, which tends, when

the two arytenoid cartilages are held apart, to rotate them so that the vocal processes are separated.

The *narrowing* of the glottis is executed by the lateral crico-arytenoids which run upwards and backwards from the antero-lateral aspect of the cricoid to the muscular processes of the arytenoid cartilages. They pull the muscular processes forwards, and thus rotate the arytenoid cartilages so as to approximate the vocal

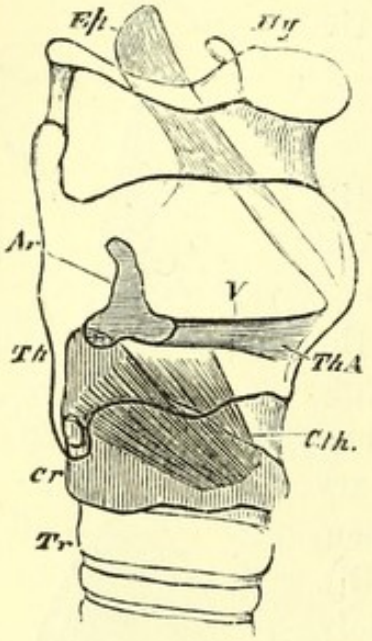


Fig. 198.—Diagram of the side view of the larynx showing the position of the vocal cords (v). (Huxley.)

Ar. Arytenoid cartilage.
Hy. Hyoid bone.
Th. Thyroid cartilage.
Cr. Cricoid cartilage.
Tr. Trachea.
C.th. Crico-thyroid muscle.
ThA. Thyro-arytenoid muscle.
Ep. Epiglottis.

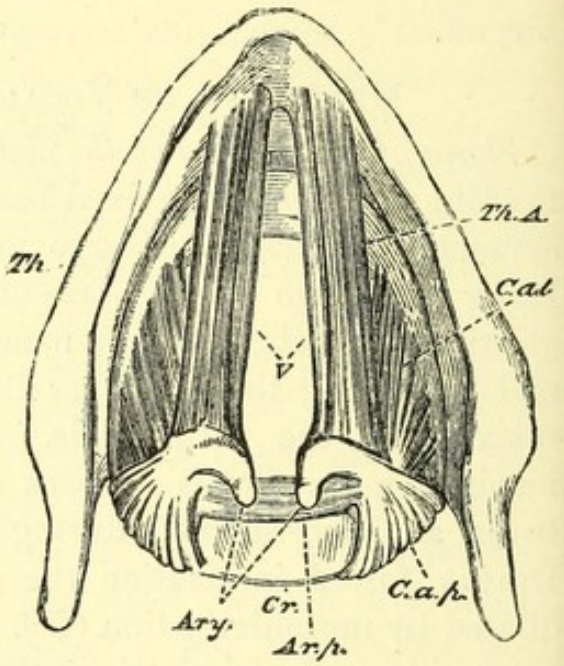


Fig. 199.—Diagram of the opening of the larynx from above. (Huxley.)

Th. Thyroid cartilage.
Cr. Cricoid cartilage.
Ary. Superior extremities of the arytenoid cartilages.
V. Vocal cords.
Th.A. Thyro-arytenoid muscles.
C.a.l. Lateral crico-arytenoid muscle.
C.a.p. Posterior crico-arytenoid muscle.
A.r.p. Posterior arytenoid muscle.

processes to one another, while any tendency towards pulling apart the bodies of the cartilages, owing to the downward direction of the muscle, is overcome by the posterior arytenoid muscle and those muscular bands which pass from the posterior surface of the arytenoid cartilages to the epiglottis and the upper part of the thyroid cartilage, the external thyro-arytenoid, and the thyro-ary-epiglottic muscles (Henle). The other fibres, which pass directly from the arytenoid to the thyroid cartilages—internal and external thyro-arytenoid muscles—in the same direction as the vocal cords, complete the

closure by helping to press together the vocal processes and by approximating the cords themselves. In spasmodic closure of the glottis, all these latter muscles act violently together, and have been grouped by Henle as the *constrictor* of the glottis.

Relaxation of the vocal cords accompanies voluntary closure of the glottis, as in holding the breath, when the false vocal cords are said to have a valvular action. The muscular fibres, which run from the arytenoid cartilages to the thyroid, nearly parallel to the true vocal cords, are those concerned in the act of relaxation when the cords are active. They pull forwards the arytenoid cartilages, and at the same time draw the upper part of the cricoid slightly forwards. These muscles have the all-important action of adapting the edges of the cords and the neighbouring surfaces to the exact shape most advantageous to their vibration.

The *tightening* of the vocal cords is caused by a single muscle, the crico-thyroid, which, on the outer side of the larynx, passes downwards and forwards from the lower part of the thyroid to the anterior part of the cricoid cartilage. It pulls the anterior part of the cricoid cartilage upwards, causing it to rotate round an axis passing through its thyroid joints. The upper part of the cricoid, which carries the arytenoids, moves backwards, the attachments of the vocal cords are separated, and the membranes are thus put on the stretch.

The requirements necessary for the production of voice are the following :—

1. *Elasticity* of the vocal cords and smoothness of their edges : freedom from all surface irregularity, such as would be caused by thick mucus adhering to them, or by any abnormality.

2. The cords must be very accurately adjusted, and closely approximated together, so that they almost touch evenly throughout their entire length.

3. The cords must be held in a *certain degree of tension*, or their vibration cannot produce any vocal tone, but only a raucous noise.

4. The air must be propelled through the glottis by a *forced expiration*. The normal expiratory current is too gentle to give the necessary vibration. After the operation of tracheotomy, the air escapes through the abnormal opening, and sufficient pressure cannot be brought to bear on the cords, so no vocal sound can be produced, and the person speaks in a whisper, unless the exit of air through the tracheotomy tube is prevented by placing the finger temporarily upon the opening.

Properties of the Human Voice.

In the voice we can recognise the properties noted in other kinds of sound. These are quality, pitch, and intensity.

(1.) The *quality* of vocal sounds is almost endless in variety, as is shown by the vocal capabilities of different individuals. The quality of any musical sound depends upon the relative power of the fundamental tone, and of the overtones that accompany it. The less the fundamental tone is disturbed by overtones, the clearer and better is the voice. This difference in quality of the human voice depends upon the perfectness of the elasticity, the relation of thickness to length, surface smoothness, and other physical conditions of the cords themselves, and the exactitude with which the muscles can adapt the surfaces. For singing well, much more is necessary than good quality of tone, which is common enough. The muscles of the larynx, thorax, and mouth must be all educated to an extraordinarily high degree.

(2.) The *pitch* of the notes produced in the larynx depends upon—first, the absolute length of the vocal cords. This varies with age, particularly in males, whose vocal organs undergo rapid growth at puberty, when vocalisation is uncertain from the rapid changes going on in the part; hence the voice is said to *crack*. The vocal cords of women have been found by measurement to be about one-third shorter than those of men, and people with tenor voices have shorter cords than basses or baritones. Secondly, on the tension of the cords: the tighter the vocal cords are drawn by the crico-thyroid muscles, the higher the notes produced; and the well-known singer Garcia believed he observed with the laryngoscope the vocal processes so tightly pressed together as to impede the vibration of the posterior part of the cords, and by this means they could be voluntarily shortened.

(3.) *Intensity* or loudness of the voice depends on the strength of the current of air. The more powerful the air-blast the greater the amplitude of the vibrations, and hence the greater the sound produced. The narrower the chink of the glottis, and the tighter the parallel cords are stretched, the less is the amount of air and the weaker is the blast required to set them vibrating; and *vice versâ*, the looser the cords and the wider apart they are, the greater the volume and the force of the air current necessary for their complete vibration. Hence it is that an intense vibration or loud note can be produced much more easily with notes of a high pitch than with very low notes, and we find singers choosing for their telling *crescendo* some note high up in the range of their voice.

The human voice, including every kind, extends over about three and a half octaves. Of this wide range a single individual can seldom sing more than two octaves. The soprano, alto, tenor, and bass forming a descending series, the range of each one of which considerably overlaps the next in the scale.

During the ordinary vocal sounds, the air, both in the resonating tubes above the larynx and in the windpipe coming from below, is set vibrating, so that the trachea and bronchi act as resonators as well as the pharynx, mouth, &c. This may be recognised by placing the hand on the thorax, when a distinct vibration is communicated from the chest wall. Such tones are, therefore, spoken of as chest notes. Besides the chest tones of the ordinary voice, we can produce notes of a higher pitch and a different quality, which are called head notes, since their production is not accompanied by any vibration of the chest wall. The physical contrivance by means of which this *falsetto* voice is brought about is not very clearly made out. The following are the more probable views :—(1) It has been suggested that in falsetto only the thin edges of the cords vibrate, the internal thyro-arytenoid muscles keeping the base of the cord fixed ; while with chest tones a greater surface of the cord is brought into play. (2) The cords are said to be wider apart in falsetto than in chest notes, and hence the trachea, &c., ceases to act as a resonator. (3) Or the cords may be arranged so that only one part of them, the anterior, can vibrate, and thus they act as shortened cords, a "stop" being placed on the point where the vibrations cease, by the internal thyro-arytenoid muscle.

The production of a falsetto voice is distinctly voluntary, and is probably dependent upon some muscular action in immediate relation to the cords, for it is always associated with a sensation of muscular exertion in the larynx as well as with changes that take place in the conformation of the mouth and other resonating tubes.

Nervous Mechanism of Voice.

The nervous mechanism by means of which vocal sounds are produced is among the most complexly co-ordinated actions that regulate muscular movements.

Like respiration, vocalisation at first seems a simple voluntary act, sounds of various kinds being produced at will by the individual. No doubt the respiratory muscles, which work the bellows of the voice organ, are under the control of the will so long as the respiration is not interfered with. The mouth and throat muscles which shape

the resonating tube are also voluntary. But the intrinsic muscles of the larynx are only voluntary in a certain sense, while in another they are distinctly involuntary, as may be seen in spasm of the larynx; for they are, in part at least, controlled by impulses which arise at the organ of hearing and pass to some co-ordinating centre, which arranges the finer muscular movements necessary to produce a certain note. When we sing a note just struck on a musical instrument, we set the expiratory, the mouth, and the special vocalising muscles in readiness, by a voluntary act, for the proper application of the air-blast; but the exact tuning of the vocal cords is accomplished, in some measure at least, reflexly by impulses arriving from the ear at a special co-ordinating nervous centre, the education of which is in advance of that of the voluntary centres, and therefore can only be controlled by the latter in persons specially educated in singing. Some persons who can sing a given note with promptness and exactitude without any effort, would find much difficulty in overcoming, by volition, the accuracy of this perfect reflex mechanism. In fact, a person with a naturally "good ear" finds it difficult to sing out of tune, even if he try.

Though we feel that we have command over the pitch of the sounds produced in the larynx, we owe much of our accuracy to the aid given by our sound-appreciating organs and the nerve centres in connection with them.

Speech.

The variations in vocal sounds which give rise to speech are not produced in the larynx, but in the throat, mouth, and nose. When unaccompanied by any vocal sound, speech only gives rise to a *whisper;* but when a vocal tone is at the same time produced, we have the ordinary loud speaking. Since vocal tones can only be produced by expiration, so we can only speak aloud by means of an expiratory current of air; but an inspiratory current may be made to give rise to a kind of whisper.

Speech is composed of two kinds of sounds, in one of which the sounds must be accompanied by a vocal tone, and are hence called "vowels;" in the other no vocal tone is necessary, but changes in shape take place in the resonating chambers, so as to give rise to noises called consonants. As the pronunciation of the consonants is always accompanied by some vowel sound, and as the difference between the vowels is brought about by changes in the shape of the mouth, the distinction between the two sets of sounds is rather artificial than real.

The production of the different vowel sounds depends upon such a change being brought about in the shape of the mouth cavity and aperture, that a resonator with a different individual note is formed for each particular vowel.

The sounds called consonants are caused by some check or impediment being placed in the course of the blast of air issuing from the air-passages. They may be classified, according to the part at which the obstruction occurs, as follows :—

1. *Labials*, when the narrowing takes place at the lips, as in pronouncing *b*, *p*, *f*, *v*.

2. *Dentals*, when the tongue causes the obstruction by being pushed against the hard palate or the teeth, as in *t*, *d*, *s*, *l*.

3. *Gutturals*, when the posterior part of the tongue moves towards the soft palate or pharynx, as in saying *k*, *g*, *gh*, *ch*, *r*.

Consonants may also be divided into different groups, according to the kind of movements which give rise to them.

1. *Explosives* are produced by the sudden removal of the obstruction, as with *p*, *d*, *k*.

2. *Aspirates* are continuous sounds caused by the passage of a current of air through a narrow opening, which may be at the lips, as in *f*, at the teeth as with *s*, or at the throat as in *ch*.

3. *Resonants* are the sounds requiring some resonance of the vocal cords, and the air current is suddenly checked by closure of the lips, as in *m*, or the dental aperture as in *n* or *ng*.

4. *Vibratory*, of which *r* is the example, requires a peculiar vibration of the vocal cords, while either the dental or the guttural aperture is partially closed.

CHAPTER XXVIII.

GENERAL PHYSIOLOGY OF THE NERVOUS SYSTEM.

Anatomical Sketch.

The nervous system includes the various mechanisms by which the distant parts of the body are kept in functional relationship with one another. By it the condition of the surroundings and the various parts of the body are communicated to a central department (cerebro-spinal axis) which in turn regulates and controls the activities of the various organs.

It is made up of two varieties of tissue, both of which possess special vital properties. The one, *nerve fibres*, composed of thread-like strands of protoplasm connects the elements of the other, *nerve corpuscles*, which form the peripheral or central terminals of the fibres. Nerve fibres are simply special conducting agents, having at one extremity a special terminal, or nerve cell, for sending impulses, and at the other end a nerve cell for receiving the impulses. These terminal organs, between which the nerve fibres pass, are the agents which determine the direction in which the impulse is to travel along the nerve. The sending organ may be at the peripheral end of the nerve, and the receiver in the nerve centres, as in the case of an ordinary cutaneous nerve, which carries impulses from the skin to the brain ; or the sending organ may be at the centre, and the receiving organ at the periphery, as in the case of the nerves conveying impulses from the brain to the muscles.

The former kind of nerves are called *afferent* carrying *centripetal* impulses, and the latter *efferent* carrying *centrifugal* impulses. Nerves are capable of carrying impulses in either direction, as has been proved by cutting the afferent lingual and the efferent hypoglossal nerves, and causing the proximal end of the former to unite with the distal end of the latter, which is distributed to the muscles of the tongue. When the union has taken place, a stimulus applied to the upper part which was normally afferent, or sensory, carries motor impulses to the muscles, *i.e.*, acts as an efferent nerve.

Protoplasm though not formed into fibres can conduct impulses, as is seen in the transmission of an impulse in textures and animals which seem to have no special conducting elements or nerve fibres. Thus in the hydra all the cells act as nerves, and in the higher animals an impulse, producing a wave of contraction, can pass from one muscle cell to the other directly, as is seen in the ureter, or in the heart of cold blooded animals.

The only essential part of a nervous conductor is a delicate proto-

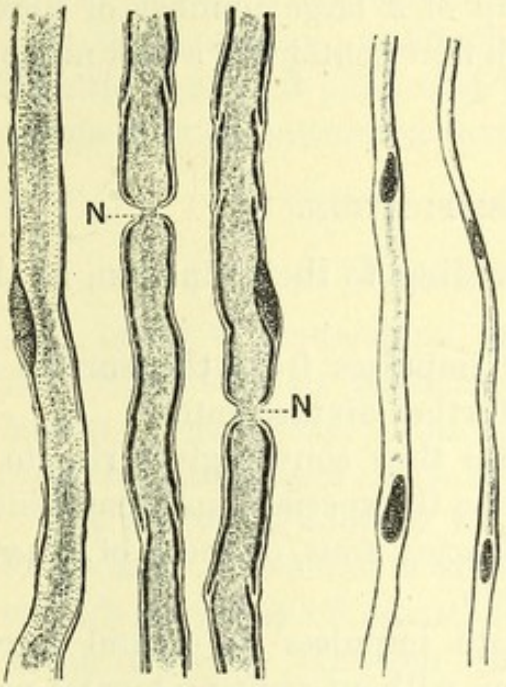


Fig. 200.—Highly magnified view of three medullated and two non-medullated nerve fibres of frog, stained with osmic acid, which makes the medullary sheath black.

N.—Nodes of Ranvier—where the axis cylinder can be seen to pass the gap in the medullary sheath.

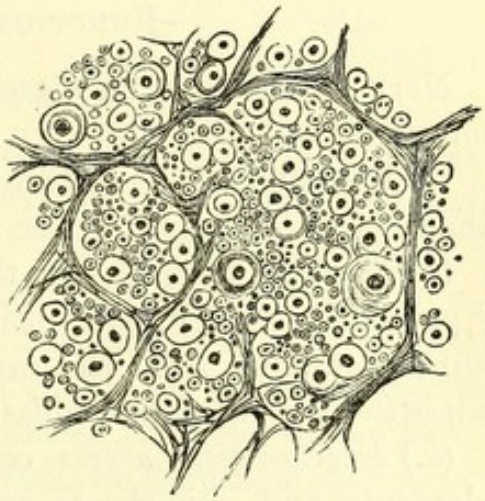


Fig. 201.—Transverse section of nerve fibres, showing the axis cylinders cut across, and looking like dots surrounded by a clear zone, which is the medullary sheath. Neuroglia separates the fibres into bundles.

plasmic fibril. Single, thin, thread-like fibrils are found carrying impulses in the nerve centres. In the nerves distributed about the body one does not meet these single protoplasmic threads (except where the fibrils are interwoven to form terminal networks, as seen in the cornea), but the fibrils are clustered together in large bundles, so as to make one nerve fibre. In the peripheral nerves this bundle of protoplasmic fibrils is covered, and is called the *axis cylinder* of the nerve fibre. In some nerve fibres there is but one very thin transparent covering, termed the *primitive sheath*, while in others there is a thick layer of doubly-refracting fluid inside the primitive

sheath, in immediate contact with the fibrils of the axis cylinder. This is called the *medullary sheath*, or white substance of Schwann, because its peculiar refractive properties make it look white when viewed in a direct light. As the nerves have or have not this medullary sheath, they have been termed "white" or "grey." The former are by far the most plentiful, since they make up the greater part of the ordinary nerves, while the grey fibres only predominate in the sympathetic nerve and its ramifications and parts of the special sense organs.

An ordinary nerve, then, is made up of a large number of fibres, held together by connective tissue, each fibre containing a vast number of fibrils within its sheath.

Functional Classification.

Nerve fibres may be classified according to their function, in the following way :—

I. Afferent Nerves which bear impulses from the surface to the nervous centres. These may be further divided into :

(*a.*) *Sensory nerves*, when the impulse they convey gives rise to a "perception." The perceptions may be the special sensations which are transmitted from the organs of *special sense*, or those of *general sensation*, giving rise to pleasure or pain.

(*b.*) *Excito-reflex nerves* communicate impulses to central nerve elements, and give rise to some action, without exciting mental perception. Such nerves regulate the viscera. According to the result of the excitation arising from their impulse they are termed—excito-motor, excito-secretory, and excito-inhibitory, &c.

(*c.*) *Mixed nerves* act as sensory and reflex nerves ; these are the most numerous, the sensory or reflex action depending upon the condition of the nerve centres.

II. Efferent Nerves, which carry impulses from the centres to the various organs throughout the body. According to the effect produced by their excitation they are termed :

(*a.*) *Motor*, conveying impulses to muscles and exciting them to contract.

(β.) *Secretory*, the stimulation of which calls forth the activity of a gland.

(γ) *Inhibitory*, when they check or prevent some activity by the impulses which they carry.

(δ) *Vaso-motor nerves*, which regulate the contraction of the muscular coat of the blood-vessels.

(ε) *Trophic, thermic, electric* nerves are also to be named, the two former being of doubtful existence, and the latter being only found in those animals which are capable of emitting electric discharges, such as electric fishes.

III. Intercentral Nerves act as bonds of union between the several ganglion cells of the nervous centres, which are connected, in a most elaborate manner, one with the other. The terminals of these fibres are possibly both receiving and directing agents, and the delicate strands of protoplasm communicating between them probably convey impulses in different directions, but of this we can have no definite knowledge, although such a supposition would aid us in forming a mental picture of the manner in which the wonderfully complete intercentral communications are accomplished.

Mode of Investigation.

In order to understand the functions of the different nerves a knowledge of their central connections and their peripheral distribution is necessary. But anatomical research unaided by experimental enquiry does not suffice to determine their function.

The procedure adopted in testing the function of a nerve is the following. The nerve is exposed and cut, and it is observed whether there be any loss of sensation or muscular paralysis in the part to which it passes. The end connected with the centres is spoken of as the central or *proximal* end, and that leading to the distribution of the nerve, is called the peripheral or *distal* end. Each of these cut ends is then stimulated, and the results are observed. If the nerve be purely motor, stimulation of the proximal end will yield no result, but when the distal end is irritated, movements follow. If, on the other hand, it be a sensory nerve, stimulation of the distal end gives no result, and that of the proximal end produces signs of pain.

Chemistry of Nerve Fibres.

The axis cylinder of nerves is probably composed, as already mentioned, of protoplasm; further than that nothing is known of its chemical properties. The medullary sheath yields certain substances which are related to the fats, and can be extracted with ether and chloroform. Among these is the peculiar compound nitrogenous fat, lecithin containing phosphorus, also cholesterin, cerebin, and kreatin.

Electric Properties of Nerves.

Like muscle, nerves may be regarded as having a state of rest and a state of activity, but the two states are not obvious in the same striking way as they are in muscle, nor do we know much of the physical properties of nerve. While at rest, however, it shows electric phenomena similar to those which have already been described as belonging to muscle tissue. These electrical currents are contemporaneous with the life of the nerve, and they undergo the same variation as occurs in muscle when the nerve passes into the active state; that is, when it transmits an impulse.

The so-called *natural current* of nerve is practically the same as that of muscle, passing in the nerve to the central part from the cut extremities of the fibre; that is to say, the current passes through the galvanometer from the electrode leading from the middle of the nerve, to that applied to the extremity. The electro-motive force of a small nerve is much less than that of a muscle. In a frog's sciatic it has been estimated to be 0·02 of a Daniell cell. The natural current of the frog's nerve is said to increase in intensity in proportion to the increase in temperature up to about 20° C., after which it decreases.

Experiments on nerve currents must be carried on with all the precautions mentioned in speaking of muscle currents, and with the non-polarisable electrodes there figured (page 381).

The Active State of Nerve-Fibres.

Nerves pass into a state of activity in response to a variety of stimuli, but their active condition cannot be readily recognized, because the only change we can detect in the nerve is that which takes place in its electric state. If it be connected with its terminals, we learn when a nerve is carrying an impulse from the results occurring in them on stimulation. In the case of an afferent nerve, we get evidence of a sensation, and when the nerve is efferent, for example, bearing impulses from the centres to the muscles, we judge of the state of activity of the nerve by the muscle contraction. For experimental purposes we use the nerve and the muscle of a frog. This *nerve-muscle preparation* is made from the leg of a frog: the sciatic nerve is carefully prepared from the thigh and abdominal cavity without being dragged or squeezed, and the gastrocnemius is separated from all its attachments except that to the femur, about two thirds of which bone is left so that the preparation may be fixed

in the clamp. In fact, the method used for the direct stimulation of muscle is also employed for the study of the excitability of nerve-fibres.

Nerve Stimuli.

Besides the normal physiological impulse which comes from the cells in connection with the nerve fibres, a variety of stimuli may excite their active state. These nerve stimuli differ little from those which are found to affect muscle, when applied directly to that tissue. They may be enumerated as follows :—

1. *Mechanical stimulation.* Almost any mechanical impulse, applied to any part of a nerve, causes its excitation. The stimulus must have a certain degree of intensity, and definite, though it may be of very short duration. If mechanical stimuli be frequently applied to a nerve in the same place, the irritability of the part is soon destroyed ; but if fresh parts of the nerves be stimulated, at each application the nerve passes into a state of tetanus, as shown by the contraction of the muscle to which it is supplied.

2. *Chemical stimulation.* Loss of water by the tissue of the nerve, whether this be caused by ordinary evaporation, or facilitated with blotting paper, exposure over sulphuric acid, or the addition of solutions of high density, such as syrup, glycerine, or strong salt solution. The application of strong metallic salts or acids ; or alcohol and ether, also a solution of bile irritates nerves ; weak alkalis, except ammonia, which has no effect on nerve, although it acts on muscle when applied directly to that tissue.

3. *Thermic stimulation* occurs when sudden changes are brought about approaching either of the extreme temperatures at which the nerve can act ; *i.e.*, near 5° or 50° C.

4. *Electric stimulation* is by far the most important for physiologists, being the most easily applied and regulated, and the least injurious to the nerve tissue. As was mentioned with respect to muscle, any sufficiently rapid change of intensity in an electric current passing through a nerve causes the molecular changes we call excitation, as shown by the muscle contracting, and the natural electric currents of the nerve undergoing variation. The less the absolute intensity of the current, the greater the effect caused by any given change in intensity. The muscle of a nerve-muscle preparation contracts, when a weak *constant current*, say from a single small Daniell cell, is suddenly allowed to pass through the nerve. This is done by placing a part of the nerve in the circuit, which is

made complete, by closing a key, when the stimulation is to be applied. This form of stimulation is called a *making shock.* While the current is allowed to pass through the nerve little or no effect is produced if the battery be quite constant. On breaking the circuit by opening the key the current suddenly ceases, and another contraction occurs, this is called the *breaking shock.* At each making and breaking of the constant current, a stimulus is applied to the nerve, and transmitted to the muscle, and it has been found that a weaker current suffices to bring about a contraction when applied to the nerve, than when applied directly to the muscle.

If a strong constant current be allowed to pass through a considerable length of a nerve for some little time, and the circuit be then suddenly broken, instead of a single contraction tetanus of the muscle results. This *breaking tetanus* (Ritter's tetanus) is easily produced when the positive pole or anode is next the muscle. Sometimes in particular conditions of the nerve, and with certain strengths of stimulation, a *making tetanus* also occurs, but more rarely and only when the negative pole is next the muscle.

When a constant current, such as we get directly from a Daniell cell, is used, that part of the nerve between the stimulating points, through which the current passes is found not to be equally affected throughout its entire length, but one single point is stimulated whence the impulse spreads. This point may be where either of the poles is in contact with the nerve ; and further, the stimulus starts from a different pole, according as the circuit is made or broken. With a *making shock* the stimulation takes place at the negative pole or *cathode*, and with a *breaking shock* at the positive pole or *anode.* That is to say the point where the current leaves the nerve is affected at the *make*, and the point where the current enters the nerve is affected at the *break* of the current.

It has been found that, other things being equal, the making shock is a more powerful stimulus than the breaking shock ; *i.e.*, a weak current will sooner cause a contraction when the circuit is made than when it is broken.

This fact that the impulse starts from the *anode* in a breaking shock is proved by means of the *breaking tetanus* just alluded to. It has been found that when the *anode* is next to the muscle the breaking tetanus is more marked and lasts longer than when the *anode* is further from the muscle than the *cathode.* When the *cathode* is nearer to the muscle than the *anode*, section of the nerve between these points during stimulation, stops the contraction at once, and no breaking tetanus occurs, because the point from which

the stimulus comes is cut off from the muscle. Intrapolar section has no effect if the anode be next the muscle, and the tetanus proceeds in a normal way, because the active pole remains in continuity with the muscle. That the stimulus occurs at the *cathode* in *making* a current may be demonstrated by the fact that it takes a certain measurable time for the impulse to travel along the nerve. If the cathode be placed as far as possible from the muscle and the anode quite near it, the contraction after a *breaking shock*, when the stimulus starts from the *anode*, will occur sooner than that which follows the *making shock*, when the stimulus starts from the *cathode*, because the impulse has a less distance of nerve to traverse in the former case.

In most experiments on nerve, a constant current, *i.e.*, one coming directly from a battery, is seldom used, because there is no ready means of regulating or varying the strength of the stimulation. The instantaneous current *induced* in one coil of wire—the *secondary coil*—by the making or breaking of a current passing through another coil—the *primary coil*—is more effective and suitable for physiological purposes. It must be remembered, however, that the induced current is both a rise and fall of electric current, *i.e.*, a make and break ; but the duration of the two changes is so small (*circa*, ·00004″) that they only act as a single stimulus. As there is no current in the secondary coil while a constant current is kept passing through the primary, of course the induced current cannot be used for experiments relating to the making and breaking shocks. The strength of the induced current being approximately in inverse proportion to the square of the distance between the two coils—moving the secondary away from the primary coil gives a ready means of varying and regulating the strength of the stimulus without any special care being devoted to the exact strength of the element used.

Du Bois Reymond's Inductorium is the instrument commonly used in physiological laboratories. In it the secondary coil can be moved away from the primary on a graduated slide, and the primary current may be made to pass through a magnetic interrupter so as to cause a rapid succession of breaks and makes, and thus give a series of stimulations one after another, which is necessary to produce tetanus. A drawing and further description of the instrument will be found at p. 386.

Velocity of Nerve Force.

It has already been stated that nerve fibres are capable of conducting impulses in either direction—*from* or *to* the nervous centres.

The position and character of the terminal organs determines the direction in which the nerve impulse usually produces results. In the ordinary peripheral nerves there are generally both kinds—efferent and afferent fibres carrying impulses in different directions.

When we reflect that the passage of an impulse along a nerve is brought about by a molecular change in the axis cylinder, we are at once struck with the rapidity with which impressions are transmitted from one part of the body to another. This velocity is, however, only relatively great. When we compare it with the velocity of the electric current or of light, we at once see how much slower the rate of nerve impulse is, and that it may be compared with rates of motion commonly under our observation. To take every-day examples :—*viz.*, nine metres per second is about the rate at which a quick runner can accomplish his 100 yards ; race-horses can gallop about 15 metres a second for a mile or so ; a mail train at full speed travels at about 30 metres a second, and the velocity of nerve force has been estimated to be in cold-blooded animals 27 metres per second ; and in man about 33 metres per second. So that the intercommunications between man's brain and the various parts of his body only travel about the same rate as an express train, and about twice as fast as the quickest horse can gallop.

Different methods may be employed for the measurement of the rate of transmission of nerve force. The simplest is, with a good myograph such as described in Chap. XVI., p. 392, to make a muscle draw two curves one over the other, in one of which the stimulation is applied to the nerve close to the muscle, and in the other, as far as possible away from it. The difference in duration of the latent period in the two curves, shown by the tuning-fork tracing, corresponds to the time taken by the impulse to travel along the part of the nerve between the two points of stimulation, the length of which can be directly measured ; and hence the velocity of the impulse estimated.

Utilising the fact that the extent of deflexion of the needle of a galvanometer is in proportion to the *duration* of a current of known strength passing through it for a short time, an accurate measurement of the difference in time of remote and near stimulation of a nerve may be made. By a special mechanism the time-measuring current is sent through the galvanometer at the same moment that the stimulating current goes through the nerve, and the instant the muscle begins to contract, it breaks the current passing through the galvanometer, so that this time-measuring current lasts only from the moment when the nerve is stimulated until the muscle begins to contract.

The Electric Change in Nerve.

Negative Variation.—The natural current of a nerve, like that of muscle, undergoes a diminution at the moment the nerve is stimulated ; this is termed the *negative variation.* It occurs with any other form of stimulation as well as when an electric shock is used, so it is not dependent on an escape of the stimulating current. In the case of a single stimulation, the negative variation is so rapidly over—lasting only ·0005 sec., that the inertia of the needle of the galvanometer prevents the change in the current being indicated. In tetanus, however, it makes a decided impression on the galvanometric needle. The strength of the negative variation depends on the condition of the nerve and the strength of the stimulus ; being stronger when the nerve is fresh and irritable and has a good natural current, and when a strong stimulus is applied.

The negative variation of the natural currents passes along the nerve from the point of stimulation in both directions, just as does the nerve impulse ; and with a galvanometer the electric change may be traced from the nerve to the muscle. It has also been shown that the negative variation travels along the nerve at the same velocity as the impulse ; namely, about 27 metres per second. Further, this rate is said to be influenced in the same way by the passage of a constant current through the nerve (to be presently described) as is the impulse derived from stimulus. These points seem to lead to the belief that the nerve impulse and the negative variation are closely related. This peculiar electric change and its accompanying impulse pass along the nerves as a kind of wave of activity, the *speed* and *duration* of which we know to be 27 metres per sec. and ·0005 of a sec. respectively ; the length of the wave we therefore calculate to be about 18 millimetres.

Electrotonus.

If one of two wires leading to a galvanometer be applied to the centre, and the other to the end of a nerve, so as to indicate the natural current, and at the same time another part of the nerve be placed in the circuit of a constant current from a battery, when the circuit of the constant (now called *polarising*) current is completed, a change is found to take place in the natural current. This is called *electrotonus.* Instead of the natural currents from the centre to the end of the nerve, a current is found to pass through the

entire length of the nerve in the same direction as the polarising current from the battery. This electrotonic current is not proportional to the strength of the natural currents, and is to be recognised when the latter are no longer to be found. It is stronger with a strong polarising current, and is most marked in the immediate neighbourhood of the poles, fading gradually away as one passes to the remoter parts of the nerve. The electrotonic state is not to be attributed to an escape of the constant polarising current, because it

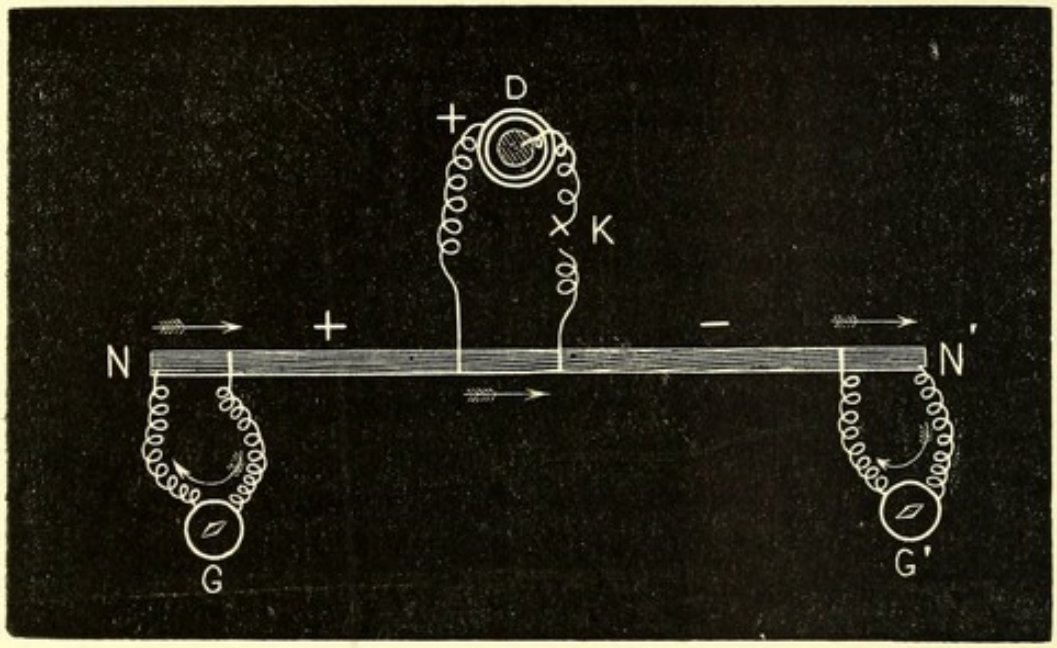


Fig. 202.—Diagram to illustrate Electrotonus.

N. N'. Portion of Nerve. G. G'. Galvanometers. D. Battery from which polarising current can be sent into nerve by closing key K. The direction of the polarising and electrotonic currents is indicated by the arrows, and is seen to be the same.

decreases gradually with the waning of the physiological activity of the nerve, and ceases at the death of the nerve long before the tissue has lost its power of conducting electric currents. It has been shown that a ligature applied to the nerve so as to destroy its physiological continuity, but not its power of carrying electric currents, prevents the passage of the electrotonic current to the part of the nerve which is thus separated.

The condition of the portion of the nerve near the anode is found to differ somewhat from that near the cathode, and hence it is found convenient to speak of the region of the anode being in the *anelectrotonic*, and that of the cathode being in the *catelectrotonic* condition. A certain time appears to be required for the production of electrotonus, a current of less duration than ·0015 of a second we are unable to detect the electrotonic state. The negative

variation must, therefore, have passed away before the electrotonus has commenced.

Irritability of Nerve Fibres.

The irritability of nerves varies according to certain conditions and circumstances. While uninjured in the body, the irritability of a nerve depends upon—

1. A supply of *blood* sufficient to provide nutriment, and to carry off any injurious effete matters that may be produced by its molecular changes.

2. A suitable amount of *rest*. Prolonged activity causes fatigue and loss of irritability, no doubt from the same causes mentioned as bringing about fatigue in muscles. The chemical changes taking place in nerves, have not yet, however, been made out with any degree of accuracy.

3. Uninjured *connection* with the nerve centres. When a spinal nerve is cut, the part connected with the periphery rapidly undergoes degenerative changes which seem to depend upon faulty nutrition, since they are accompanied by structural changes—fatty degeneration. This appears to commence in a very short time after the section—often in about three to five days. The part of the nerve remaining in direct connection with the cord, retains its irritability for a very much longer time.

In the artificial stimulation, by means of electric shocks applied to the nerve of a cold-blooded animal, there are many minor conditions which have considerable influence on the irritability, as evidenced by the response given by the attached muscle to weak stimuli. The more important of these are :—

1. *Temperature* changes. In the case of a frog's nerve, a rise of temperature to 32° C. causes an increase in its excitability. Also a fall of temperature below zero tends to make the nerve more easily excited. Both these conditions have, however, a very fleeting effect, for the nerve soon dies at the temperatures named, and probably the increased irritability is only to be taken as a sign of approaching death. It thus appears that a medium temperature is the optimum for nerve work.

2. The *part* of the nerve stimulated, is also said to have some effect on the result of a given strength of stimulus. The further from the muscle, the more powerful the contraction produced, other things being equal. So that the impulse is supposed to gather force as it goes, as in the case of a falling body, and hence has been spoken of as the *avalanche* action of nerve impulse.

3. A *new section* of the nerve is said to increase its irritability, as does, indeed, any slightly stimulating influence, such as drying, and chemical or mechanical meddling of any kind. This increase in irritability probably depends upon injurious changes going on in the nerve, as the influences just alluded to lead to complete loss of excitability if carried too far.

4. The *electrotonic state.*—The most remarkable changes in the excitability of a nerve, are those brought about by the action of a constant current passing through the nerve, so as to set up the conditions just described as *anelectrotonus* and *catelectrotonus.*

The irritability of the nerve is increased in the region near the cathode, and is diminished in the neighbourhood of the anode.

The increase of irritability is in proportion to the intensity of the

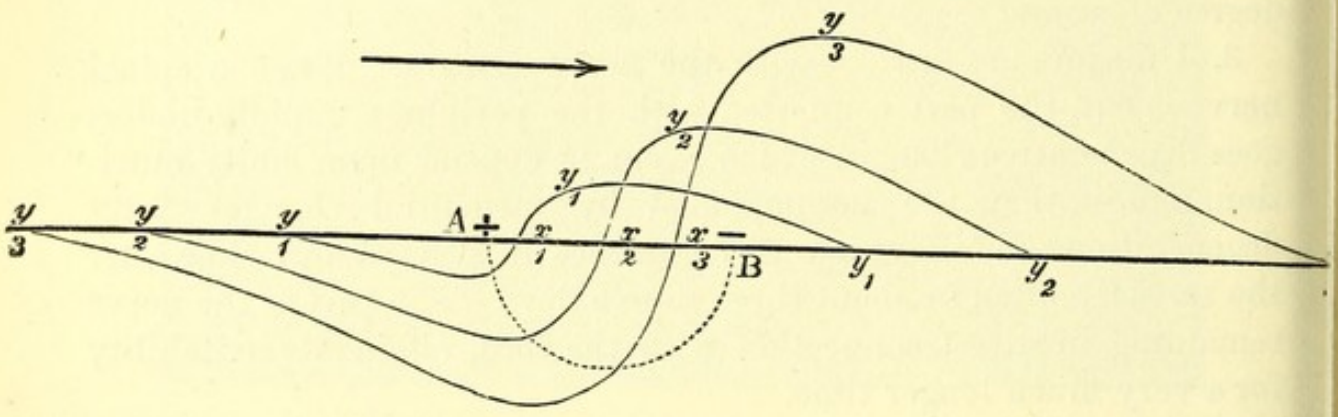


Fig. 203.—Diagram illustrating the variations of irritability of different parts of a nerve during the passage of polarising currents of varying strength through a portion of it.

A = Anode; B = Cathode; AB = Intrapolar district; y^1 = Effect of weak current. y^2 = Effect of medium current. y^3 = Effect of strong current.

The degree of change effected in the irritability of the part is estimated by the distance of the curves from the straight line. The part of curve below the line corresponds to *decrease*, that above to *increase* of irritability. Where the curves cross the line is called the indifferent point. With strong currents this approaches the cathode. (From Foster after Pflüger.)

catelectrotonic and the decrease in proportion to the intensity of the anelectrotonic state. Thus the increase is most marked in the immediate neighbourhood of the cathode, and fades with the distance from the negative pole; and similarly, the decrease is strongest at the anode, and becomes less and less as it passes away from the positive pole. In the same way, in the part of the nerve between the two poles—the intrapolar region—the decrease and increase of irritability become less marked towards the middle point between the cathode and the anode, so that here we find an unaffected part, which has been called the *indifferent point.*

It is a remarkable fact that this indifferent point is not always midway between the two poles, but decreases its distance from the cathode in proportion as the polarising current is made stronger. That is say, with strong polarising currents the indifferent point is near the cathode (B) ; with weak currents it lies near the anode (A) (Fig. 203).

Besides becoming less irritable in proportion as the polarising current becomes more powerful, the anelectrotonic region of the nerve loses its ability to conduct impulses, and may finally, with a very strong current, even when applied for a short time, become quite incapable of conducting an impulse.

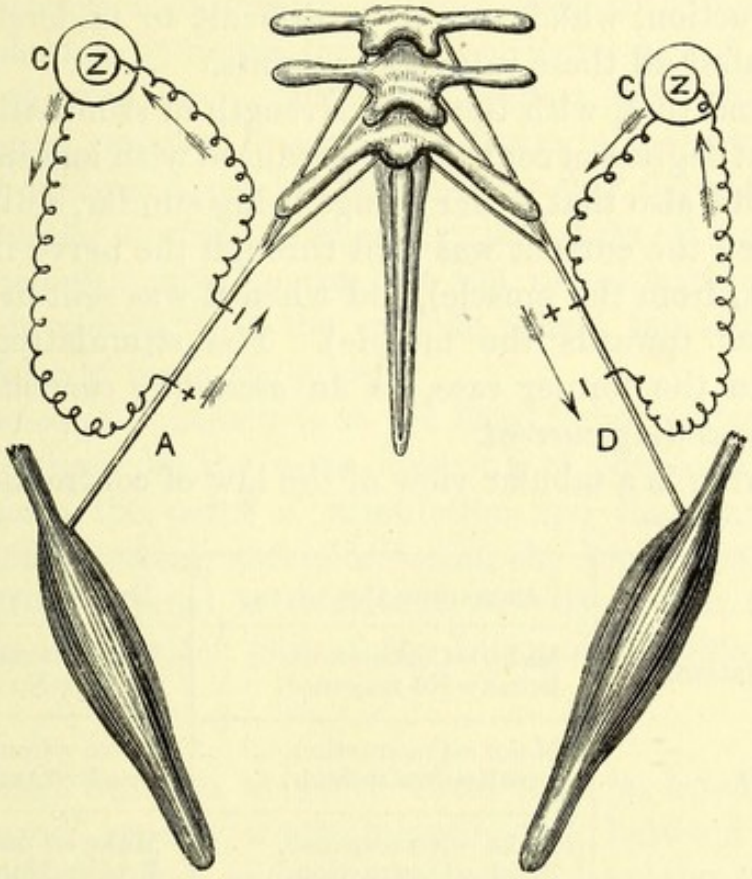


Fig. 204.—Diagram to show the meaning of the terms *ascending* and *descending* currents, used in speaking of the law of contraction. The end of the vertebral column, sciatic nerves and calf muscles of a frog are shown.

The arrows indicate the direction of the *ascending current* A, *on the left*, and the *descending current* D, *on the right*, according as the positive pole of the battery C, is below or above.

If the polarising current be now opened, so as to stop its passage through the nerve, and remove the anelectrotonic and the catelectrotonic states, a kind of rebound occurs in the condition of both the altered regions, and the part which has just ceased to be catelectrotonic, and was, therefore, over-irritable, becomes, by a kind of negative

modification, very much lowered in its irritability ; while on the other hand, the anelectrotonic part, by a positive rebound, becomes more excitable than in its normal state. The rebound over the line of normal irritability lasts a very short time ; but as we shall see presently, it is of greater duration than the passage of the negative variation along the nerve.

The Law of Contraction.

Upon the foregoing facts, and others already mentioned—*viz.*, that the impulse starts in the nerve from different poles and with different force, with a making and a breaking shock—depends the law of contraction, which would be difficult to understand without bearing in mind all these interesting points.

It was found that, with the same strength of stimulation, not only were different degrees of contraction produced with making and breaking shocks, but also that, other things being similar, a different result followed when the current was sent through the nerve in an upward direction (*i.e.*, from the muscle), and when it was sent in a downward direction (*i.e.*, towards the muscle). The stimulating current is spoken of, in the former case, as an *ascending current*, and in the latter as a *descending current.*

The following is a tabular view of the law of contraction :—

	Ascending Currents.	Descending Currents.
Weak Stimulation.	Make = Contraction. Break = No response.	Make = Contraction. Break = No response.
Medium ,,	Make = Contraction. Break = Contraction.	Make = Contraction. Break = Contraction.
Strong ,,	Make = No response. Break = Contraction.	Make = Contraction. Break = No response.

To explain this law the following points must be kept in view :—

1. In a breaking shock, it is the *disappearance* of *anelectrotonus* which causes the stimulation to start from the anode.
2. In a making shock it is the *appearance* of *catelectrotonus* which causes the stimulation to start from the cathode.
3. With the same current the *make* is more powerful than the *break.*
4. Anelectrotonus causes *reduction* of irritability and conductivity of the nerve.

5. Catelectrotonus causes *increase* of irritability and conductivity of the nerve.
6. With *ascending currents* the part of the nerve next the muscle is in a state of reduced functional activity (anelectrotonus).
7. With *descending currents* the part of the nerve next the muscle is in a state of exalted activity (catelectrotonus).
8. The reduction or exaltation of activity is much greater with strong currents.

That only making shocks cause contraction with very weak currents, simply depends on the greater efficacy of the entrance of catelectrotonus into the nerve, which causes the making stimulation.

That contraction follows in all four cases, with medium stimulation, is explained by assuming that the depression of the functional activity of the nerve is not sufficient to affect its conductivity.

The want of response to a making shock, in the case of the strong descending current, depends upon the fact that the part of the nerve near the muscle, around the anode, is in a state of lowered activity, and is, therefore, unable to conduct the impulse which has to pass through this region from the cathode, where the stimulation takes place, in order to reach the muscle.

The absence of contraction at the breaking of a strong descending current, is caused by the same lowering of the conductivity of the nerve between the point of stimulation and the muscle, because at the cessation of strong catelectrotonus, the region near the cathode rebounds from exalted to depressed activity, and at the moment of stimulation the greater part of the intrapolar region is an electrotonic.

The special function of nerve fibres may be briefly stated to be their power of rapidly intercommunicating between distant parts. The axis cylinder has undergone a special development, by which it is enabled to conduct impulses much more quickly than ordinary protoplasm. Even muscle tissue transmits impulses about thirty times more slowly than a nerve fibre. A highly organised animal body, without nerve fibres, would be in a worse condition than a highly organised state without a telegraphic or even a postal system.

Nerve Corpuscles or Terminals.

These are the real actors in the nervous operations, while the fibres are merely their means of communicating with one another. One

set of terminals is placed on the surface of the body and is adapted to the reception of the various external influences which are brought to bear on it from without by its surroundings. These receivers of extrinsic stimuli are necessarily much varied so as to be capable of appreciating all the different kinds of stimulation presented to them. They are either distributed over the entire surface so as to meet with general mechanical and thermic changes, or they are further specialised for the reception of luminous, sonorous, odorous or gustatory impulses. In the latter cases the special terminals are collected into one part, and form complex organs, which will be described presently in the chapters on the special senses.

Another set of terminals is placed in the deeper textures, where

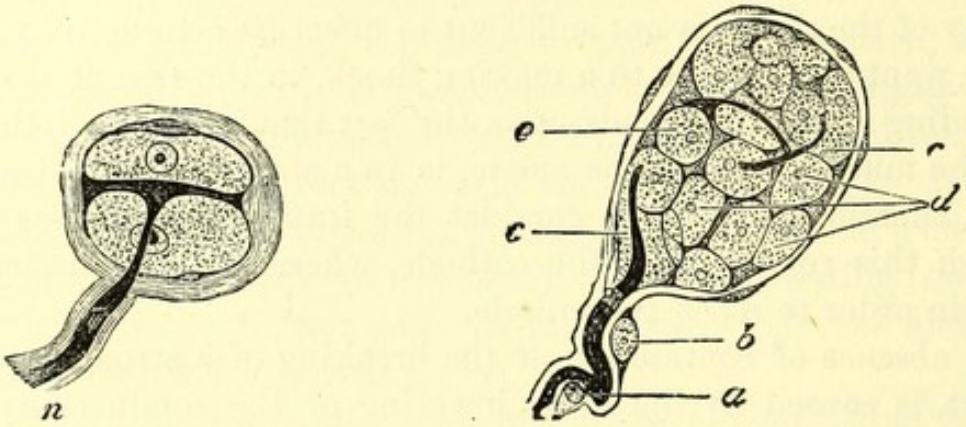


Fig. 205.—Tactile nerve endings, composed of small capsules, in which the black axis-cylinder of the nerve (a), and (n) meets with many protoplasmic units.

they act as local distributing agents; such as the nerve plates on skeletal muscles, and the ganglionic networks in the wall of the intestine. In many instances, however, the exact mode of connection between the nerve and the protoplasm of the tissue elements, to which it bears impulses, has not been satisfactorily made out. In the remaining class of nerve terminals the cells are grouped together so as to form larger and smaller colonies, and more definitely deserve the name of nerve or ganglion cells. These are the central terminals, and are placed either in the cerebro-spinal axis, or in swellings of the nerves called sporadic ganglia.

Of these nerve cells there are many varieties, all of which have the following characteristics. The cells are of considerable size and have processes branching off from them, by means of which they communicate with the nerve fibres. These processes may be single or many, hence they are spoken of as uni-, bi-, or multi-polar cells, &c. The nucleus is commonly very distinct, and contains a

well-marked nucleolus. The abundant protoplasm, which is usually contained in a delicate cell wall, is in direct connection with the axis cylinder of the nerve fibres, with which it communicates by means

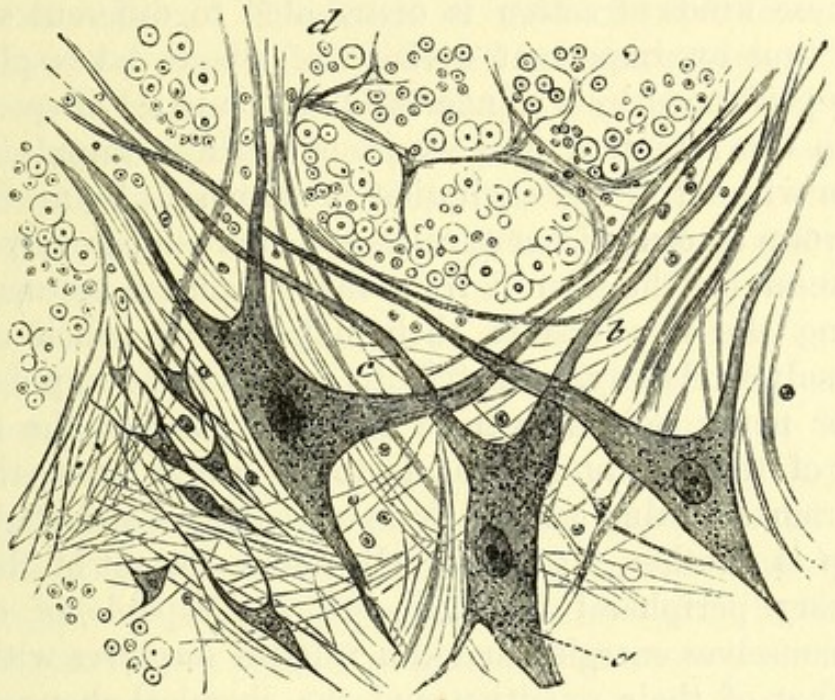


Fig. 205*.—Multipolar cells from the anterior grey column of the spinal cord of the dog-fish (*a*) lying in a texture of fibrils; (*b*) prolongation from cells; (*c*) nerve-fibres cut across. (Cadiat.)

of thin strands of protoplasm that pass out from the cell by the processes. A delicate striation of the protoplasm may sometimes be recognised, indicating the course of the nerve fibrils as they run into the cells from the processes.

The Functions of Nerve Cells.

Any mass of living protoplasm, such as an amœba, can receive extrinsic stimuli, which affect directly its conditions, and though the impression may be very localised in its application, yet all the parts of the cell participate in the sensation, and probably take part in the resulting movement.

Besides those acts of which we can recognise the cause, many others occur in amœbæ which we are not able to trace to any definite cause other than the energies derived from its special powers of assimilation. We say that not only can an amœba feel local stimulation, transmit the impulse to remoter parts of its body, and respond by movement to the stimulus, but it can also *initiate* impulses which appear as motions, &c., as the result of intrinsic processes of a

chemical nature. We may conclude from this fact alone that automatic action is one of the properties of protoplasm derived from its proper chemical activities.

In the nerve centres of all the more complex animals we find that each of these kinds of action is distributed to different varieties of cells, and thus an important division of labour takes place. The first act is performed by a wonderfully elaborate set of special organs adapted to the reception of the various extrinsic impulses or sensations from without. The excitation is then sent by nerve fibres to another group of central nerve cells, which are apparently employed solely in receiving the stimuli from the peripheral organs, and then distributing the impulses to their neighbours, which can direct, modify, analyse, classify, re-distribute, or check the impulses, so that the higher nerve cells may have less work, and at the same time lose none of the advantage that is to be gained from the income derived from stimulus coming from without. Connected with the last group is another, the nerve cells which lie out of the reach of the ordinary peripheral impulses, but are capable of developing within themselves energies, and can initiate impulses with no other aid than that of their nutrition and the chemical changes resulting from their assimilation.

These impulses are distributed to the peripheral active tissues, muscles, glands, &c., probably through the medium of other sets of cells analogous to the last group situated in the nerve centres as well as to the local distributors which act as unions between the other textures and the nerve fibres.

The functions of nerve cells which form centres of action may be classified thus:—

1. Reflexion. Many cells are capable of reflecting impulses received from an afferent nerve; that is to say they send it by an efferent nerve to some active tissue, such as a muscle or gland. This kind of direction is spoken of as a simple *reflex action*. For instance, if a grain of red pepper be placed on the tongue, an impulse soon travels from the peripheral receiving terminal, along an afferent nerve to its central terminal, which reflects the impulse to the efferent nerve, going to the salivary gland, and the result is an increased secretion of saliva.

2. Co-ordination. There are but few reflex acts that do not require the co-operation of several cells, and these work together in an orderly manner, the resulting activity being well arranged and usually adapted to some purpose. The first act of the receiving cells of a reflex centre must then be to distribute and direct the

impulse into those channels which lead to groups of cells capable of sending impulses in an orderly and definite direction. This directing and arranging power is spoken of as *co-ordination*, and probably is an attribute common to all nerve cells.

3. AUGMENTATION. The force of the reflected efferent impulse bears a direct relation to the afferent impulse as determined by the strength of the stimulus. Thus if the amount of pepper on the tongue be much increased, not only is the flow of saliva greater, but the excitation spreads from one central cell to another until the neighbouring centres are affected. Thus we often find the lachrymal glands are influenced by very strong stimulation of the tongue, and pour out their secretion, as is said, "in sympathy" with the mouth glands. But the amount of the afferent impulse is not the only factor in determining the energy of response to be reflected along the efferent channels. Some nerve cells have a distinct power of increasing the amount of response to a given stimulus. When an irritant falls near the mucous membrane in the neighbourhood of the laryngeal opening, a very different result is produced. The greater response to an equal stimulus in such cases probably depends rather on a peculiar *augmenting* power of some central cells than upon any special local mechanisms.

4. INHIBITION. Under certain conditions, which will be more fully explained presently, nerve cells appear to have the power of restraining the activity of other cells or tissues, of checking their receptive or executive power, or lessening the impulse reflected so as to produce less effect, this is called *inhibition*.

5. AUTOMATISM. Nerve cells are supposed to have the power of originating activity, *i.e.*, discharging impulses without receiving any exciting impulses from other nervous agencies that we can find out. Examples may be found among those carrying on operations which require to be of a more or less permanent kind, such as the partial contraction of the muscle cells of the arteries. *Automatic actions* are sometimes classified as those acting continuously and those that undergo rhythmical changes. If carefully examined, most of the so-called constant automatic actions will be found to show traces of rhythmic relaxation. The centre governing respiratory movement is an example of an automatic group of cells. Impulses are discharged from it even when the connections with all the afferent nerves which influence it normally are cut off, and it has no other excitant than the warm blood supplying it with nutriment. Respirations are, however, normally regulated by a reflex mechanism, the channels of which reside in the vagus nerve.

In the nerve cells we must also seek *mental activity*, under which term may be considered perception, volition, thought, and memory. It is very difficult to allocate the due proportions of reflexion, co-ordination, augmentation, inhibition, automatism, &c., requisite for the development of mental faculties. In all probability what we call mental operations are related to activities called forth as the resultant of a long series of external and internal excitations, modified by intrinsic nutritive influences, acting upon innumerable groups and complex associations of nerve cells, the general outline of whose function and tendency of action, *character*, has been rough-hewn by hereditary transmission.

CHAPTER XXIX.

SPECIAL PHYSIOLOGY OF NERVES.

Spinal Nerves.

The thirty-one pairs of nerves which leave the vertebral canal by the openings between the vertebræ are called spinal nerves, in contradistinction to the cranial nerves, which pass through the base of the skull. They are attached to the spinal marrow by two bands, the *anterior* and *posterior roots*, which unite together in the intervertebral canal to form the trunk of the nerve. Just before the junction of the two roots the posterior one is enlarged by a ganglionic swelling.

The spinal nerves are all "mixed nerves," that is to say, they contain both efferent and afferent fibres; but these two sets of fibres are separate in the roots of each nerve, the posterior root containing only afferent, and the anterior only efferent fibres. The spinal nerves are thus joined to the spinal marrow by two nervous cords, each one of which is functionally distinct. About seventy years ago Charles Bell discovered that the anterior roots were motor, and the posterior sensory channels. Hence, the anterior are commonly spoken of as the *motor roots*, and the posterior as the *sensory roots* of the spinal nerves. The experiments to show this difference are simple, but require delicate manipulation.

If the *anterior roots* of the nerves supplying the hind leg of a recently-killed frog be divided, the muscles of the limb are cut off from the centres in the spinal cord, and the leg hangs limply, and does not move if pinched when the frog is suspended; whereas the limb on the sound side, upon which the anterior roots are intact, will move energetically when the motionless one is irritated. If the distal ends of the divided anterior roots be stimulated, the muscles of the paralysed limb are thrown into action; but stimulation of the proximal end gives no result. If the two webs of this frog be compared, the blood-vessels running across the transparent part of the web on the injured side will be found to be fuller than those in

the web of the other limb, but if the distal ends of the motor roots are stimulated, the dilated blood-vessels return to their normal calibre. By these experiments we are shown that efferent fibres carrying impulses to the muscular walls of the vessels are contained in the anterior roots of the spinal nerves together with fibres to the skeletal muscles.

Posterior roots.—The fact that when the leg on the side where the anterior roots have been severed is stimulated, the animal moves the other, is sufficient to show that the sensory connections between its surface and the cord are not destroyed by cutting those anterior roots; and we may conclude—taking the other facts just mentioned into account—that the afferent fibres are situated in the posterior roots.

We can confirm this result by cutting the posterior roots on one side of a recently-killed frog, and repeating the stimulation of the feet.

Pinching the limb whose posterior roots are cut, gives rise to no response, because the impulses cannot reach the spinal cord; but stimulation of the sound foot causes obvious movements of both legs. This shows that the section of the posterior roots of one limb cuts off the afferent (sensory) communication on the side operated on, but that the efferent (motor) impulses can pass freely to the muscles, even when the posterior roots are divided, for the limb moves on pinching the other foot. If the proximal ends of the cut posterior roots be stimulated, motions are produced showing that the centres in the spinal cord are influenced by the afferent impulses carried by those posterior roots. If the distal ends of the cut roots be stimulated no movement results.

Recurrent fibres.—It has been sometimes found that stimulation of the anterior roots seemed to cause pain, as shown by the motion of other parts besides those to which this root was distributed; and it was believed that some sensory fibres must run in the anterior roots. But it has been found that if the corresponding posterior roots be cut these signs of pain when the anterior roots are stimulated are not shown. From this it has been concluded that the apparent sensory channels of the motor roots are nothing more than some sensory fibres which pass from the nerve trunk a little way up the motor root, and then turn back and descend again to the junction of the roots, whence they pass along the posterior root to the cord. These fibres are named the "recurrent sensory fibres," and the recurrent sensibility of the anterior roots is not regarded as any serious departure from Bell's law.

The course of the secretory, &c., nerves probably follows that of the motor channels at their exit from the cord. Their peripheral dis-

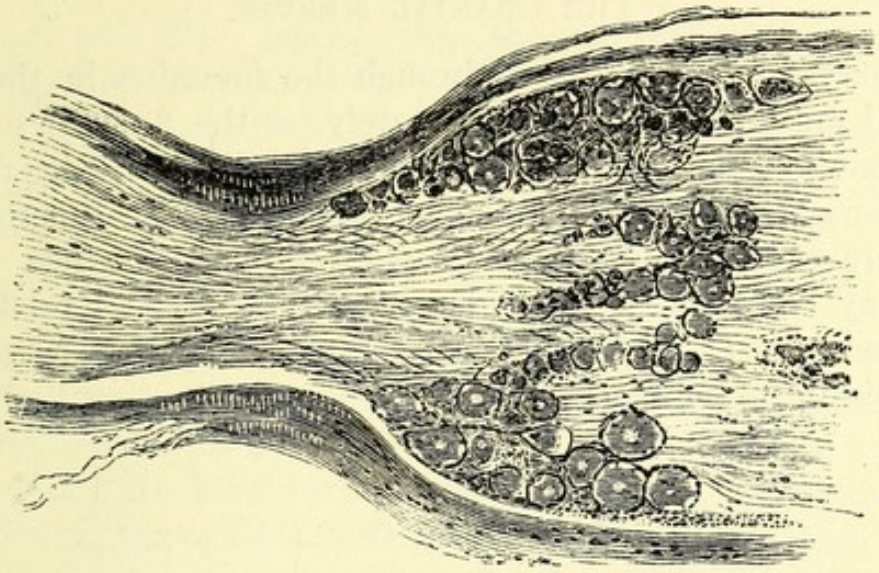


Fig. 206.—Section through spinal ganglion of a cat, showing ganglion cells interspersed between the fibres. (Low power.)

tribution, and that of the vaso-motor nerves, are intimately connected with the sympathetic system, and will be considered further on.

Of the function of the *ganglia* on the posterior roots of the spinal nerves but little is positively known. There is no evidence of their being centres of reflex action, nor can they be shown to possess any marked automatic activity. From the fact that when a mixed nerve is divided the end cut off from the ganglion degenerates after a few days, these ganglia are supposed to preside over the nutrition of the tissue of the nerve itself. And if the roots be cut, that part of the posterior root attached to the cord degenerates, while the piece connected with the ganglion is well nourished. This is not the case if the anterior root be divided, but, on the contrary, that portion next the cord is well nourished, while that connected with the posterior root is degenerated.

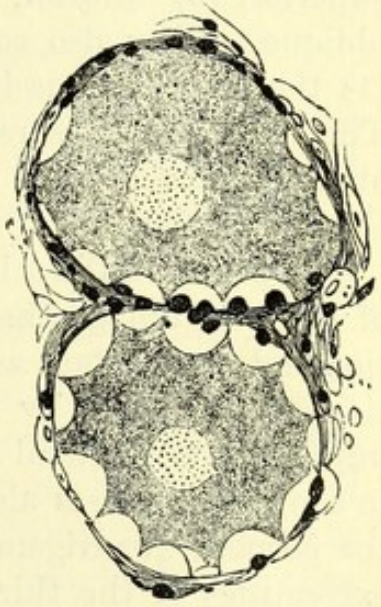


Fig. 207.—Two cells from the former seen under a high power, showing the fine protoplasm here and there retracted from the cell-wall.

It would thus appear that the trophic function of the ganglia is restricted to the sensory nerves, while the nutrition

of the motor nerves is provided for by nervous centres situated higher up.

The Cranial Nerves.

The nerves which pass out through the foramina in the base of the skull must be considered separately, as the function of each of them shows some peculiarity. Some are exclusively nerves of special sense, some are simple, being purely motor in function, while others are exceedingly complex, containing many kinds of fibres. They may be taken in the order of their functional relationships, motor and mixed. Those which relate to the special senses will be considered in future chapters.

III.—The Motor Oculi Nerve.

The nerves of the third pair are efferent, being the chief motor nerves of the eyes. They arise from the grey matter on the floor and roof of the aqueduct of Sylvius, pass out of the brain substance near the pons from between the fibres of the peduncle, and run between the posterior cerebral and superior cerebellar arteries. They pass into the orbits in two branches, and are distributed to the following orbital muscles :—(1) elevator of the eyelid ; (2) the superior, (3) inferior, and (4) internal recti, and (5) the inferior oblique. They also contain fibres which carry efferent impulses to (1) the circular muscle of the iris, and to (2) the ciliary muscle. The latter branches reach the eye by a short twig from the inferior oblique branch, which goes to the ciliary ganglion, and thence enters the ciliary nerves.

The action of the orbital muscles is, in the main, under the control of the will, though they afford good examples of peculiar co-ordination and involuntary association of movements. The reflex contraction of the pupil by the action of the circular muscle (sphincter pupillæ) is a bilateral act, the afferent impulse of which originates in the retina, passes along the optic nerves, and is transmitted, from the corpora quadrigemina, to both the third nerves. The central extremities of the third nerves must have an intimate connection with each other and with the optic nerves, for the diminution in size of both pupils follows accurately the increase in intensity of the light to which even one of the retinæ is exposed. In retinal blindness and after section of the optic nerve the pupil becomes dilated from loss of the retinal excitation. The action of the ciliary muscle may be said

to be voluntary, since we can voluntarily focus our eyes for near or far objects. Contraction of the sphincter pupillæ and of the internal rectus is associated with the contraction of the ciliary muscle in accommodation.

Section of the third nerve within the cranium gives rise to the following group of phenomena :—(1.) Drooping of the upper lid (Ptosis). (2.) Fixedness of the eye in the outer angle (Luscitas). (3.) Dilatation and immobility of pupil (Mydriasis). (4.) Inability to focus the eye for short distances.

IV.—The Trochlear Nerve.

This thin nervous filament arises under the Sylvian aqueduct, and passes into the superior oblique muscle, to which it carries voluntary impulses, which are involuntarily associated with those of the other muscles moving the eyeball. Paralysis of this muscle causes no very obvious impairment in the motions of the eyeball when the head is held straight, but it is accompanied by double vision, so there must be some displacement of the eyeball. When the head is turned on one side the eye follows the position of the head instead of being held in its primary position. In paralysis of this nerve a double image is seen only when looking downwards, and the image on the affected side is oblique and below that seen by the sound eye.

VI.—The Abductor Nerve of the Eye.

This arises in the floor of the fourth ventricle, and appears just below the pons Varolii. It is the motor nerve of the external rectus muscle of the eye. Paralysis or section of it causes inward squint.

VII.—(Portio Dura) Motor Nerve of the Face:

This nerve arises from a grey nucleus in the floor of the fourth ventricle. It passes with the other part of the seventh (portio mollis) or auditory nerve into the internal auditory meatus of the temporal bone. It first passes out towards the hiatus, then turns at a right angle to form a knee-like swelling (geniculate ganglion), and then runs backwards along the top of the inner wall of the drum, and passing downwards through a special canal in the bone, comes out at the stylo-mastoid foramen, and finally spreads out on the side of the face. It is essentially an efferent nerve, being partly motor and partly secretory, though its connections have caused afferent

functions to be ascribed to it. Its distribution may be thus briefly summarised :—

i. *Motor fibres.*—(1.) To the muscles of the forehead, eyelids, nose, cheek, mouth, chin, outer ear, and the platysma, which may be grouped together as the *muscles of expression.* (2.) To some muscles of *mastication*, viz., buccinator, posterior belly of digastric, and the stylohyoid—all the foregoing being supplied by external branches—while in the temporal bone it gives a branch to (3) the *stapedius* muscle, and also a branch from the geniculate ganglion named the great superficial petrosal nerve, which after a circuitous course is supplied to the elevator and azygos muscles of the palate and uvula.

ii. *Secretory fibres.*—(1.) To the parotid gland by the small superficial petrosal nerve, which sends a branch to the otic ganglion, whence the fibres pass to the auriculo-temporal nerve, and then on to the gland. (2.) To the sub-maxillary gland by the chorda tympani, which after having traversed the tympanum leaves the ear by a fissure at its anterior extremity, then joins the lingual branch of the fifth to separate from it and pass into the sub-maxillary ganglion which lies in close relation to the gland (compare figs. 64 and 65).

iii. Vaso-motor, or vaso-inhibitory influences, are chiefly connected with the motor and secretory functions, since dilatation of the vessels of muscles and glands accompanies the motion and secretion that follows stimulation of the nerves going to them.

iv. The following afferent impulses are said to travel along the track of the portio dura and its branches :—(1.) Special taste-sensations, which are chiefly located in the chorda tympani branch, may be explained by the branches of communication which pass from the trunk and petrous ganglion of the glosso-pharyngeal to the portio dura at its exit from the foramen, or by the connection in the drum of the ear between the tympanic branch of the glosso-pharyngeal and the geniculate ganglion of the portio dura through the lesser superficial petrosal nerve. (2.) Ordinary sensations, which are also located in the chorda tympani, are said to traverse this nerve in an afferent direction until it comes near the otic ganglion, when the sensory fibres leave the chorda and pass to the inferior division of the fifth nerve through the otic ganglion.

Injury of the facial nerve in any of the deeper parts of its course gives rise to the striking group of symptoms known as facial paralysis, the details of which are too long to be given here. When it is remembered that muscles aiding in expression, mastication, deglutition, hearing, smelling, and speaking, are paralysed, and that taste, salivary

secretion, and possibly ordinary sensation are impaired, one can form some idea of the complex pathological picture such a case presents.

V.—N. Trigeminus, or Tri-facial Nerve.

This nerve transmits both efferent and afferent impulses carried by two different strands of fibres. The motor part, which arises from a grey nucleus in the floor of the fourth ventricle, is much the smaller of the two, and has been compared to the anterior root of a spinal nerve. The large sensory division springs from a very extensive tract, which can be traced from the pons Varolii through the medulla to the lower limit of the olivary body, and on to the posterior cornua of the spinal marrow. This set of fibres has been linked to the posterior root of a spinal nerve, being somewhat analogous to it in origin, function, and the fact that there is a large ganglion on it within the cranium.

The distribution and peripheral connections of this nerve are somewhat complicated, and should be carefully studied when the manifold functions of its branches are being considered. The various impulses conveyed by the tri-facial nerves may be thus enumerated :—

i.—Efferent Fibres.

1. *Motor.*—To the muscles of (1) mastication, viz., temporal masseters, both pterygoids, mylohyoid, and the anterior part of the digastrics ; (2) to the tensor muscle of the soft palate ; and (3) to the tensor tympani. (4) In some animals (rabbit) nerve filaments are said to pass to the iris, reaching the eyeball by the ciliary ganglion.

2. *Secretory.*—The efferent impulses which stimulate the cells of the lachrymal gland to increased action, pass along the branches of the ophthalmic division of this nerve.

3. *Vaso-motor.*—The nerves governing the muscles of the blood vessels of the eye, of the lower jaw, and of the mucous membrane of the cheeks and gums.

4. *Trophic.*—On account of the impairment of nutrition of the eye and mucous membrane of the mouth, which occurs after injury of fifth nerve, it is said to carry fibres which preside over the trophic arrangements of these parts.

ii.—Afferent Fibres.

1. *Sensory.*—All the divisions of the tri-facial nerve may be said to be connected with cutaneous nerves, by which the ordinary sensory impulses are carried from—(1) the entire skin of the face, and the anterior surface of the external ear; (2) from the external auditory meatus; (3) from the teeth and periosteum of the jaws, &c.; (4) from the mucous membrane lining the cheeks, floor of the mouth, and anterior part of the tongue; (5) from the lining membrane of the nasal cavity; (6) from the conjunctiva, ball of the eye, and orbit generally; (7) and from the dura mater including the tentorium.

2. *Excito-motor.*—Some of the fibres which have just been enumerated as carrying ordinary sensory impressions, have special powers of exciting co-ordinated reflex motions. Thus the sensory fibres from the conjunctiva and its neighbourhood are the afferent channels in the common reflex acts of winking and closing the eyelids; and the fibres from the nasal mucous membrane excite the involuntary act of sneezing.

3. *Excito-secretory.*—As in the case of reflex movements, secretion may be excited reflexly. Fibres carry afferent impulses to the medulla from the anterior part of the tongue, and excite activity of the salivary glands. Stimulation of the mucous membrane of the nose or eye causes impulses to pass to the secretory centre of the lachrymal glands, which are frequently thus reflexly excited.

Intense stimulation of almost any of the afferent nerves may excite these reflex phenomena. Thus the most stoic person will experience active secretions of saliva and lachrymal fluid, as well as spasmodic closure of the lids during the extraction of a tooth. Even the bold use of a blunt razor will cause tears to flow down the cheeks, by sending excito-secretory impulses along the branches of the inferior and superior maxillary division of this nerve.

4. *Tactile impulses* are appreciated by the anterior part of the tongue with remarkable delicacy, and are conveyed by the lingual branch of the fifth nerve; most of the cutaneous fibres are also capable of receiving tactile stimulation.

5. *Taste.*—The tastes appreciated by the anterior part and the edges of the tongue are carried by fibres which lie in the peripheral branches of this nerve. These belong chiefly, if not altogether, to the chorda tympani, and leave this lingual branch of the fifth to join the seventh nerve on their way to the trunk of the glosso-pharyngeal.

There are four ganglia in close relation to the branches of the fifth nerve which have certain points of similarity, and may, therefore, be considered together, although their positions show that they are engaged in the performance of very different functions.

We have not yet been able to ascertain the value of these little points of junction of motor, sensory, vaso-motor, and secretory fibres, because, so far, we are unable to attribute to the cells of the ganglia either reflecting or controlling action, or any automatic power.

They all have efferent (motor and secretory) and afferent (sensory) connections with the nervous centres, and also connections with the main channels of the sympathetic nerves. These are spoken of as the roots of the ganglia. Their little branches are generally mixed nerves.

The Ciliary or Ophthalmic Ganglion.

This ganglion lies in the orbit. It has three roots, which come from—(1) the inferior oblique branch of the third nerve, by a short slip, which forms the motor root; (2) from the nasal branch of the ophthalmic division of the fifth, and (3) from the carotid plexus of the sympathetic. The branches go mostly to the ball of the eye, and may be divided into afferent and efferent. The afferent are sensory branches, connecting the cornea and its neighbouring conjunctiva with the centres. The efferent fibres go to the iris and cause dilatation of the pupil (coming mostly from the sympathetic), and the vaso-motor fibres going to the choroid coat, iris, and retina.

The Sphenopalatine or Nasal Ganglion.

This lies on the second division of the fifth nerve, from which it gets its sensory root. Its motor root comes from the seventh by the great superficial petrosal nerve, and its sympathetic root from the carotid plexus by the branch joining this nerve. These enter the ganglion together, and are spoken of as the vidian nerve. Afferent (sensory) impulses, from the greater part of the nasal cavity, pass through this ganglion. Its efferent branches are—(1) motor to the elevator of the soft palate and azygos uvulæ; (2) vaso-motor, which comes from the sympathetic; and (3) secretory, which supply the glands of the cheek, &c.

Otic or Ear Ganglion.

The otic ganglion lies under the foramen ovale, where the interior division of the fifth comes from the cranium. Its roots are—(1) motor ; (2) sensory, from the inferior division of the fifth ; and (3) sympathetic, made up of a couple of fine filaments from the plexus, around the meningeal artery. By its branches it communicates with the seventh, chorda tympani, and sends filaments to the parotid gland.

The Submaxillary Ganglion.

This is on the hyoglossus muscle in close relation to the lingual branch of the fifth, from which it gets a sensory root. The chorda tympani passes to the ganglion, carrying efferent impulses through it to the gland. Its sympathetic branches come from the plexus around the facial artery.

VIII.—The Glosso-pharyngeal Nerve.

This nerve forms part of the eighth pair, and springs from the floor of the fourth ventricle above the nucleus of the vagus. It is a mixed nerve, the functions of which may be thus classified.

Afferent fibres, which are of various kinds, viz. :—

(1.) *Sensory fibres*, carrying impulses from the anterior surface of the epiglottis, the base of the tongue, the soft palate, the tonsils, the Eustachian tube and tympanum.

(2.) *Excito-motor*. This nerve excites important reflex movements in swallowing and vomiting, when a stimulus is applied to the glosso-palatine arch.

(3.) *Excito-secretory*, the stimulation of the back of the tongue gives rise to a copious flow of saliva by means of reflex action.

(4.) *Taste* sensations are, for the most part, carried by this nerve ; they are conveyed from special nerve-endings in the back of the tongue (see Taste).

The *efferent fibres* are not so varied, being simply *motor* to the middle constrictor of the pharynx, stylo-pharyngeus, elevator of the soft palate, and the azygos uvulæ.

The Spinal Accessory Nerves.

These also form part of the eighth pair of nerves, and arise from the medulla oblongata and spinal cord, as low down as the seventh

cervical vertebra. The lower fibres leave the lateral columns at their posterior aspect, and then run up between the denticulate ligament and the posterior roots of the spinal nerves to enter the cranial cavity. On their way out of the cranium they divide into two parts, one of which becomes amalgamated with the vagus, and the other passes down the side of the neck as the motor nerve of the sterno-mastoid and trapezius muscles. Physiologically, it may be compared with the anterior root of a spinal nerve, and the part accessory to the vagus probably supplies that nerve with most of its motor branches.

The Vagus Nerve.

The vagus arises from the lower part of the floor of the fourth ventricle, and is connected with many of the important groups of nerve cells in this neighbourhood.

The functions of its widely-distributed fibres may be thus briefly stated :—

A. The Efferent Fibres may be divided into—

1. *Motor-nerve* channels, going to a great portion of the alimentary tract and air-passage ; the following muscles getting their motor supply from the branches of the vagus—the pharyngeal constrictors, some muscles of the palate, œsophagus, stomach, and greater part of the small intestine. Motor impulses also pass along the trunk of the vagus—though leaving the cord by the roots of the accessory nerve—to the intrinsic muscles of the larynx ; these fibres lie in the inferior or recurrent laryngeal nerve except that to the crico-thyroid, which lies in the superior laryngeal branch. The tracheal muscle and the smooth muscle of the bronchial walls are also under the control of the pulmonary branches of the vagus.

2. *Vaso-motor fibres* are said to be supplied to the stomach and small intestine. These fibres are probably derived from some of the numerous connections with the sympathetic.

3. *Inhibitory impulses* of great importance for the regulation of the forces of the circulation pass along the vagus to the ganglia of the heart. As already explained in detail (see p. 227), these fibres are always acting, as shown by the fact that section of the vagi causes a considerable quickening of the heart-beat. On the other hand, if the distal end of the cut vagus be stimulated, the heart beats more slowly, and in some animals may come to a standstill in a condition of relaxation.

B. The AFFERENT FIBRES still more widely spread, are important for the functions of the various viscera. They are :—

1. *Sensory fibres* carrying impulses from the pharynx, œsophagus, stomach, and intestine, and from the larynx, trachea, bronchi, and lungs generally. The pneumonia which follows section of the vagi depends on—(1) the removal of sensibility, and the ease with which foreign matters can enter the air-passages ; or (2) the violent breathing necessary when the motor nerves of the larynx are cut ; or (3) the injury of trophic or vaso-motor fibres.

2. *Excito-motor nerves.* There is no nerve that can be compared with the vagus in the variety of reflex phenomena in which it participates. Afferent fibres in this nerve cause spasm of the muscles of the glottis and thorax and govern the respiratory rhythm, preside over inhalation of air and excite the expiratory muscles. Thus irritation of the mucous membrane at the root of the tongue, the folds of the epiglottis, larynx, trachea, or bronchi, causes spasmodic fits of coughing. Irritation of the pharyngeal or the gastric fibres gives rise, by reflex stimulation, to the act of vomiting.

Stimulation of the proximal cut end of the trunk of the vagus causes inspiratory effort and cessation of breathing movements in the position of inspiration. Stimulation of the central cut end of the superior laryngeal branch, causes reflex spasm of the muscles of the larynx and a fixation of the expiratory muscles in the position of expiration. The fibres which regulate the respiratory rhythm consist of two sets, probably passing from the lungs to the inspiratory and expiratory centres, and causing each to act before its ordinary automatism would transmit any discharge of impulse to the thoracic muscles.

In the laryngeal branches are fibres which bear centrifugal impulses to the vaso-motor centres in the medulla, and excite them to action. These, which may be grouped with the excito-motor channels, are spoken of as "*pressor*" fibres, from the influence they exert upon the pressure of blood in the arteries.

3. *Excito-inhibitory* fibres pass from the heart to the vaso-motor centre. Stimulation of these fibres, which take somewhat different courses in different animals, checks the tonic action of the vaso-motor centre, and greatly reduces the blood pressure. Hence these fibres form the *depressor nerve.* Its terminals in the heart are stimulated by distension of that organ ; and the vaso-motor centre is thereby inhibited, the arteries dilate and the blood pressure falls so that the over-filled heart can empty itself.

4. *Excito-secretory fibres.* Stimulation of the gastric endings of the

vagus causes not only gastric, but also salivary secretion, which occurs as a precursor of gastric vomiting.

Section of both vagi in the neck causes the death of the animal within a day or two after the operation, and the following changes may be observed while it lives:—1. The heart-beat is much quicker as shown by the increased pulse-frequency. 2. The rate of breathing is very much slower. 3. Deglutition is difficult, the food easily passing into the air-passages through the insensitive larynx.

Section of the superior laryngeal nerves is followed by slight slowness of breathing, loss of sensibility in the larynx, entrance of food into the air-passages, chronic broncho-pneumonia, and death.

Section of the inferior laryngeal nerves gives rise to the same final result, because the muscles of the larynx are paralysed, and closure of the glottis is impossible. A change in voice follows the section or injury of even one inferior laryngeal, as may often be seen in man from the effect of the pressure of an aneurism.

IX.—Hypoglossal Nerve.

This nerve appears in the furrow between the olivary body and the anterior pyramid, on a line with the anterior roots of the spinal nerves. It corresponds with the anterior roots in function, being a purely motor nerve. It bears impulses to the muscles of the tongue, and others attached to the hyoid bone.

Some sensory fibres lie in its descending branch, but these are probably derived from the vagus or tri-facial nerves, with which its branches inosculate.

It is also said to contain the vaso-motor fibres of the tongue.

Section of the nerves causes paralysis of the muscles of the tongue; when this is unilateral, the tongue inclines to the injured side, while being protruded from the mouth; but while being drawn in, it passes to the sound side. This is easily understood when it is borne in mind that the two acts depend upon the intrinsic muscles of the tongue, bringing about an elongation or shortening of the organ respectively.

CHAPTER XXX.

SPECIAL SENSES.

It has been pointed out that the afferent or sensory nerves receive impressions at the surface of the body, and carry the impulses to nerve cells in the brain where they give rise to *sensation*. The afferent nerves are the means by which the mind becomes acquainted with occurrences in the outer world, and also the channels along which the impulses pass to reflex nerve centres whence they are sent to different parts, without causing any sensation in the nerve cells of the sensorium.

The ordinary sensory nerves are in such relationship to the surface that they are affected by slight mechanical and thermal stimuli, which throw them into activity and send impulses to the brain. But we are capable of appreciating many other impressions besides those excited by the ordinary sensory nerves. We feel the character of a surface by touch, and we distinguish between degrees of *heat* and *cold*, when the difference is far too slight to act as a direct nerve stimulus. We can appreciate *light*, of which no degree of intensity is capable of exciting a nerve fibre to its active state, or of stimulating an ordinary nerve cell in the least degree. We recognise the delicate air-vibrations called *sound*, which would have no effect on an ordinary nerve ending. We can also distinguish several *tastes;* and finally, we are conscious of the presence of incomprehensibly small quantities of subtle odours floating in the air. When the amount of the substance is too small to be recognised even by spectrum analysis, which detects extraordinarily minute quantities, we can perceive an odour by our olfactory organs.

There must then be a special apparatus for the reception of each of these impressions in order that the nervous system may be accessible to such slender influences. In fact special mechanisms must exist by means of which the quality of a surface, heat, light, sound, taste, and odour are enabled to act as nerve stimuli. These nerve terminals

are known as the special sense organs, the physiology of which is at the same time the most difficult and most interesting branch of study in Biological Science.

The nerve-fibres which carry the impulses from the various organs of special sense do not differ from other nervous cords, so far as their structure and capabilities are concerned. The special peripheral end organs are connected with nerve cells in the brain, the sole duty of which is to receive impulses from a special sense organ and distribute them to the brain-centres so that they may cause a special sensation. By whatever means a nerve trunk from a special sense organ be stimulated, its impulse excites the special sensation usually arising from stimulation of the special organ to which it belongs. Thus electric stimulation of nerves in the tongue causes a certain taste ; mechanical or other stimulation of the optic nerve-trunk gives rise to the sensation of flashes of light, and a distinct odour may be caused by the presence of a bony growth, pressing upon the olfactory nerve.

The capability of the nerve centres connected with the nerves of special sense to give rise to a special sensation, is called their *specific energy*. And the special influence, light, sound, &c., which alone suffices to excite the special peripheral terminal, and which the given terminal alone can convert into a nerve stimulus, may be called its *specific* or *adequate stimulus*.

Although we habitually think of the sensation as if coming from the surface where the stimulus is applied, it is really only developed in the centres in the brain. Thus we say we feel with our skin, hear with our ears, and see with our eyes, &c., whereas these are only the parts from which the nerve impulses, giving rise to the specific energy, pass to the feeling, hearing, or seeing regions of our cerebral cortex. This is obvious from what has been already said of the nerve fibres of the special sense organs. If the nerve be cut no sensation is excited, though adequate stimulus reach the organ of special sense ; and if a stimulus be applied to the nerve trunk a similar sensation is produced, as if the specific stimulation had operated on the special nerve terminal from which these fibres habitually carried impulses. This peripheral localisation of cutaneous sensations is really accomplished in the mind, just as by a mental act of a different character, the impressions communicated by the eye are projected into the space about us in our thoughts, instead of being referred to the retina, or thought of as being produced in the eye itself. This power of the sensorium to localise impressions to certain points of the skin, and to project into space

the stimulation caused by the light reflected from distant objects, so as to get a distinct and accurate idea of their position, is the result of experience and habit, which teach each individual that when a certain sensation is produced, it means the stimulation of a certain point of the skin, and that the objects we see are not in our eyes, where the impulses start, but at some distance from us. We learn this from a long series of unconscious experiments carried on in our early youth by movements of the eyes with co-operation of the hands. Even the sensations which arise in the various centres of the sensorium, as the result of internal or central excitations, are from habit attributed to external influences, and thus we have various hallucinations and delusions, such as seeing objects or hearing sounds which may only depend on the excitation of certain groups of cells in the cortex of the brain.

The sensations produced in our nerve centres as the result of the afferent impulses coming from our special sense organs give rise to a form of knowledge called *perception*. Each perception helps to make up our knowledge of the outer world and of ourselves. Without this power of perception we could have no notion of our own existence and no ideas of our surroundings; in fact we should be cut off from all sources of knowledge and be idiots by deprivation of all intelligence from without.

A complete special sense apparatus may be said to be made up of the following parts :—

1. A special nerve-ending only capable of being excited by a special *adequate stimulus*.

2. An afferent nerve to conduct the impulses from the special end-organ to the nerve centre.

3. Central nerve cells, capable by *specific energy* of translating the nerve impulse into a *sensation*, which is commonly referred to some local point of the periphery.

4. Associated nerve centres, capable of *perceiving* the sensations, forming *notions* thereon, and drawing conclusions, from the present and past perceptions, as to the intensity, position, quality, &c., of the external influence.

Skin Sensations.

The sensations arising from many impulses coming from the skin are grouped together under the name of the *Sense of Touch*. This special sense may be resolved into a number of specific sensations, each of which might be considered as a distinct kind of feeling, but s usually regarded as simply giving different qualities to the sensa-

tions excited by the skin. These sensations are :—(1) *Tactile Sensation*, or sensation proper, by means of which we appreciate a very gentle contact, recognise the *locality* of stimulation, and judge of the position and form of bodies ; (2) the sense of *pressure;* and (3) the sense of *temperature.*

The variety of perceptions derived from the cutaneous surface, and the large extent of surface capable of receiving impressions, make the skin the most indispensable of the special sense organs, though we value this source of our knowledge but little. If we could not place our hands as feelers on near objects to investigate their surfaces, &c., we should lose an important source of information that has contributed largely to our visual judgment. We think we know by the look of a thing what we originally learned by feeling it. If our conjunctiva did not feel, we should miss its prompt warning, and our voluntary movements could not protect our eyes from many unseen injuries that normally never trouble us. If the skin were senseless it would require constant mental effort to hold a pen, and our power of standing and walking would be most seriously impaired. And how utterly cut off from the outer world should we be, were we incapable of feeling heat and cold.

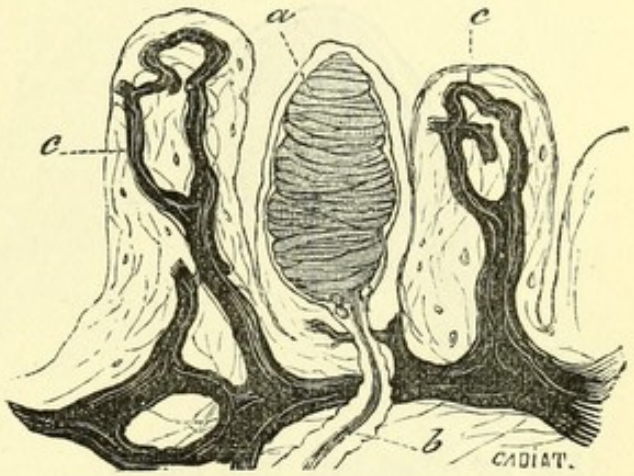


Fig. 208.—Drawing from a section of injected skin, showing three papillæ, the central one containing a tactile corpuscle (*a*), which is connected with a medullated nerve, and those at each side are occupied by vessels. (Cadiat.)

Nerve-Endings.

Although the end-organs of the nerves of the skin are the simplest of all those belonging to the apparatus of special sense, yet we have a very imperfect knowledge of their immediate relationships to the different qualities of touch impressions. We know of several different nerve-endings apparently adapted to the reception of certain impressions, but of the exact kinds of stimuli that affect these different terminals we are ignorant.

The peripheral terminals of the sensory nerves, like the other

special sense organs, are usually composed of modified epithelial cells, into close relation to which the axis cylinders of nerves can be traced. They may be thus enumerated :—

1. The *Touch-corpuscles* (Meissner) are egg-shaped bodies situated in the papillæ of the true skin, underlying directly the epithelial cells of the rete mucosum. They occupy almost the entire papilla. The nerve fibres seem to be twisted around the corpuscle in a spiral manner, while the axis cylinders enter the body, and the covering of the nerve becomes amalgamated with its outer-wall. The touch-corpuscles vary in size in different parts of the skin ; usually being

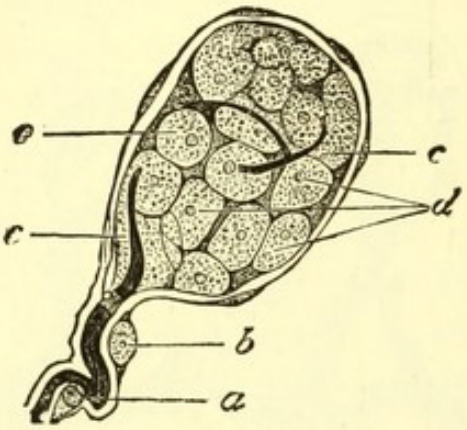


Fig. 209.—End bulb from human conjunctiva, treated with osmic acid, showing cells of core. (Longworth.)
a, Nerve fibre ; *b*, nucleus of sheath ; *c*, nerve fibre within core ; *d*, cells of core.

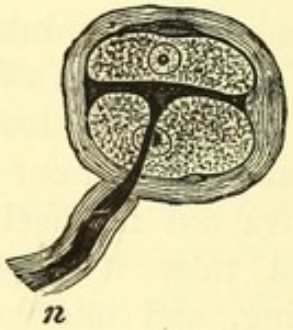


Fig. 210.—Tactile corpuscle from a duck's tongue, containing two tactile cells between which lies the tactile disc. (Izquierdo.)

larger where the papillæ in which they lie are well-developed. The axis cylinders are said to end in swellings called tactile cells.

2. *End-bulbs* (Krause) are smaller than the last and are less generally distributed over the surface of the body, being localised to certain parts. They are chiefly found in the conjunctiva and mucous membranes of the mouth and external generative organs. They consist of a little vesicle containing some fluid ; a few large nucleated cells. The axis cylinder terminates between the cells, the membrane which forms the vesicle of the bulb being fused with the sheath of the nerve. Many different shapes and varieties of these bodies have been described, but there seems to be no definite morphological or physiological distinction between the varieties.

3. *Touch-cells* (Merkel) found in the deeper layers of the epidermis of man as well as in the tongues of birds, are large cells of the epi-

thelial type with distinct nuclei and nucleoli. Frequently they are grouped together in masses and surrounded by a sheath of connective tissue; in which condition they resemble touch-corpuscles.

4. *Free nerve-endings* occur on the surface of the epithelium of the mucous membranes, and are seen on the surface of the cornea (Cohnheim). Here delicate, single strands of nerve fibrils can be seen after gold staining, passing between the epithelial cells and ending at the surface in very minute blunted points or knobs.

Naked nerve-fibrils have also been traced into the deeper layers of the epidermis of the skin, where they end among the soft cells of

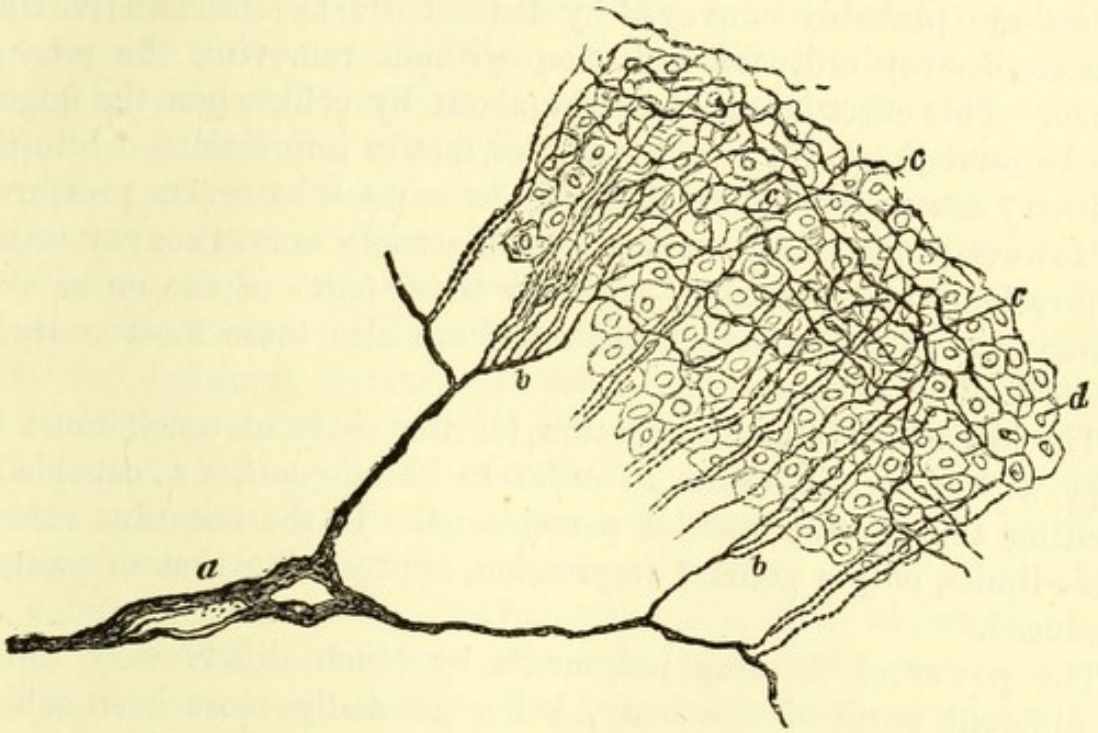


Fig. 211.—Drawing of termination of nerves on the surface of the rabbit's cornea. *a*, Nerve fibre of sub-epithelial network; *b*, Fine fibres entering epithelium; *c*, Intra-epithelial network. (Klein.)

the mucous layer, either in branched cell-like bodies (Langerhans), or delicate loops (Ranvier).

In the subcutaneous fat-tissue and in parts remote from the surface some sensory nerves terminate in large bodies, easily visible to the naked eye, called—

5. *Pacinian corpuscles.* They are ovoid bodies made up of a great number of concentrically arranged layers of material, of varying consistence, with a collection of fluid in the centre, in which an axis cylinder ends. There is no doubt that they are the terminals of afferent nerves, but if they are connected with the sense of touch, which is doubtful from their distribution, it is unknown to what

special form of sensation they are devoted. From their comparatively remote relation to the skin, lying some distance beneath it and not in it, like the other endings mentioned, they are probably connected with the appreciation of pressure sensations rather than those more properly called tactile.

The sense of touch must be carefully distinguished from ordinary sensibility or the capability of feeling pain, which is not a *special* but a *general* sensation, and is received and transmitted by different nerve channels. This we know from the facts, that the mucous passages in general can receive and transmit painful but not tactile impressions, and that in the spinal cord the sensory and tactile impulses are probably conveyed by distinct tracts. Certain narcotic poisons destroy ordinary sensation without removing the sense of touch. This effect is also brought about by cold, when the fingers are benumbed, gentle contact excites tactile impressions, while the ordinary sensations of pain can only be aroused by severe pressure.

However, most of the nerves we call sensory nerves convey tactile impressions, and speaking generally those parts of the outer skin which have the keenest tactile sense are also those most ready to excite feelings of pain.

The intensity of the stimulation for the sense of touch must be kept within certain limits in order to be *adequate*, *i.e.*, capable of exciting the specific mental perceptions. If the stimulus exceed these limits, only a general impression, approaching that of pain, is produced.

The power of forming judgments by touch differs very much in different parts of the body, being generally most keen where the surface is richest in touch corpuscles, namely, the palmar aspect of the hands and feet, and especially the finger-tips, tongue, lips, and face.

When we feel a thing in order to learn its properties, we make use of all the qualities of which our sense of touch is made up. We estimate the number of points at which it impinges on our finger-tips, rub it to judge of smoothness, press it to find out its hardness, and at the same time gain some knowledge of its temperature and power of absorbing heat.

To get a clear idea of our complex sense of touch we must consider each kind of impression separately.

Sense of Locality.

By this is meant our power of judging the exact position of any point or points of contact which may be applied to the skin.

Thus if the point of a pin be gently laid on a sensitive part of the skin we know at once when we are touched, and if a second pin be applied in the same neighbourhood, we feel the two points of contact and can judge of their relative position. When we feel anything, we receive impulses from many points of contact bearing varied relationships to each other, and thus become conscious of a rough or smooth surface.

The delicacy of the sense of locality differs very much in different parts of the skin. It is most accurate in those parts which have been used as touch organs during the slow evolution of the animal kingdom.

The method of testing the delicacy of the sense of locality is that of applying the two points of a compass to different parts of the skin, and, by varying their position, experimentally determine the nearest distance at which the two points give rise to distinct sensations. The following precautions must be attended to in carrying out this experiment. 1. The points must be simultaneously applied, or two distinct sensations will be produced at abnormally small distances. 2. The force with which the points are applied must be equal and minimal, because excessive pressure causes a diffusion of the stimulus and a blurring of the tactile sense. 3. Commencing with greater and gradually reducing the distance of the points enables a person to appreciate a less separation than if the smaller distances were used at first. 4. The duration of the stimulus; two points of contact being distinguished at a much nearer distance if the points be allowed to rest on the part, than when they are only applied for a moment. 5. The temperature and material of the points should be the same. 6. Moisture of the surface makes it more sensitive. 7. Previous or neighbouring stimulation takes from the accuracy of the sensations produced. 8. The temperature of the different parts of the skin should be equal, as cold impairs its sensibility.

The following table gives approximately the nearest distances at which some parts, which may be taken as examples of the more and less sensitive regions of the skin, can recognize the points of contact by their giving rise to two distinct sensations :—

Tip of the tongue	1 mm.
Palmar aspect of the middle finger-tip .	2 „
Tip of the nose	4 „
Back of the hand	15 „
Plantar surface of great toe . . .	18 „

Fore arm, anterior surface . . .	40 mm.
Front of thigh	55 „
Over ensiform cartilage	50 „
Between scapulæ	70 „

If one point of the compass be applied to the same spot, and the other moved round so as to mark out in different directions the limit at which the points can be distinguished as separate, we get an area of a somewhat circular form, for which the name *sensory circle* has been proposed. It would be convenient to explain this on the simple anatomical basis that the impressions of this area were carried by one nerve-fibre to the brain, and thus but one sensation could be produced in the sensorium. We know this cannot be the true explanation, from the following facts. 1. No such anatomical relationship is known to exist. 2. By practice we can reduce the area of our sensory circles in a manner that could not be explained by the development of new nerve-fibres. 3. If the two points of the compass be placed near the edges of two well-determined neighbouring sensory circles, and so in relation with the terminals of two nerve-fibres, they will not give distinct impressions ; they require to be separated as much as if they were applied within the boundary of one of the circles where they also give rise to the double perception.

To explain better the sense of locality it has been supposed that sensory circles are made up of numerous small areas, forming a fine mosaic of *touch-fields*, each of which is supplied by one nerve-fibre, and that a certain number of these little fields must intervene between the stimulating points of the compasses in order that the *sensorium* be able to recognize the two impulses as distinct. For, although every touch-field is supplied by a separate nerve-fibril which carries its impulses to the brain, and is therefore quite sensitive, the arrangement of the cells in the sensorium is such that the stimuli carried from two adjoining touch-fields are confused into one sensation. Thus, when an edge is placed on our skin, we do not feel a series of points corresponding to the individual fields with which it comes in contact, but the confusion of the stimuli gives rise to an uninterrupted sensation, and we have a right perception of the object touched.

The Sense of Pressure.

There seems to be a reason for separating the perception of differences in the degree of pressure exercised by a body from the simple

tactile or local impression. If we support a part of the body so that no muscular effort be called into play in the support of an increasing series of weights placed upon the same area of skin, we can distinguish tolerably accurately between the different weights. It has been found that if a weight of about 30 grammes be placed on the skin a difference of about 1 gramme can be recognized—that is, we can distinguish between 29 and 30 grammes, if they are applied soon after one another. If the weights employed are smaller, a less difference can be detected ; if larger weights are used the difference must be greater, and it appears that the weight-difference always bears the same proportion to the absolute weight used. We can perceive a difference between $7\frac{1}{4}$ and $7\frac{1}{2}$, $14\frac{1}{2}$ and 15, 29 and 30, 58 and 60, &c., the discriminating power decreasing in proportion as the absolute degree of stimulation increases.

One of the reasons why the sense of pressure is regarded as distinct from that of locality is that the former is found not to be most keenly developed in the parts where the impressions of locality are most acute. Thus judgment of pressure can be more accurately made with the skin of the fore-arm than the finger-tip, which is nine times more sensitive than the former to ordinary tactile impressions, while the skin of the abdomen has an accurate sense of pressure though dull to ordinary tactile sensation.

It has been said above that the weights by which pressure-sense is to be tested should be applied rapidly one after the other. This fact depends upon the share taken in the mental judgment by the function we call memory. In a short time the recollection of the impression passes away and there no longer exists any sensation with which the new stimulation can be compared.

At best we can form but imperfect judgments of pressure by the skin impressions alone. When we want to judge the weight of a body we poise it in the free hand, which is moved up and down so as to bring the muscles which elevate it into repeated action. Hereby we call into action a totally different evidence, namely, the amount of muscle power required to raise the weight in question, and we find we can arrive at much more accurate conclusions by this means. The peculiar recognition of how much muscular effort is expended is commonly spoken of as *muscle-sense*, which may arise from a knowledge of how much voluntary impulse is expended in exciting the muscles to action, but more probably it depends upon afferent impulses arriving at the sensorium from the muscles. By its means we aid the pressure-sense in arriving at accurate conclusions of the weight of bodies, so that in the free hand we can distinguish between 39 grm. and 40 grm.

Temperature Sense.

We are able to judge of the difference in temperature of bodies which come in contact with our skin. Since our sensations have no accurate standard for comparison we are unable to form any exact conception of the absolute temperature of the substances we feel. The sensation of heat or cold, derived from the skin itself, without its coming into contact with anything but air of moderate temperature, varies with many circumstances, and because of these variations the powers of judgment of high or low temperature must be imperfect. The skin feels hot when its blood-vessels are full; it feels cold when they are comparatively empty. An object of constant temperature can thus give the impression of being hot or cold according as the skin itself is full or empty of warm blood. But independent of any very material change in the blood-supply of the cutaneous surface of a part, any change in the temperature of its surroundings causes a sensation of change of temperature, which is, however, a purely relative judgment. Thus if the hand be placed in cold water, we have at first the sensation of cold; to which, however, the skin of the hand soon becomes accustomed and no longer feels cold; if now the hand be placed in water somewhat warmer—but not higher in temperature than the atmosphere—we have a feeling of warmth. If the hand be placed in as hot water as the skin can bear, it feels at first unpleasantly hot, but this feeling soon passes away and the sensation is comfortable. If from this hot water it be placed again in the water of the air temperature, this—which before felt warm—feels very cold.

An important item in the estimation of the temperature of an object by the sensations derived from the skin depends upon whether it be a good or a bad conductor of heat. Those substances which are good conductors, and therefore, when colder than the body, quickly rob the skin of its heat, are said to feel cold, whilst badly-conducting bodies, of exactly the same temperature, do not feel cold. It is then the rapid loss of heat that gives rise to the sensation of cold.

The power of the skin in recognizing changes of temperature is very accurate, although the power of judging of the absolute degree of temperature is very slight.

By dipping the finger rapidly into water of varying temperature it has been found that the skin can distinguish between temperatures which differ by only $\frac{1}{4}^\circ$ Cent. or $\frac{1}{2}^\circ$ Fahr. The time required for the arrival of temperature impressions at the brain is remarkably long when compared with the rate at which ordinary tactile impulses

travel. To judge satisfactorily of the temperature of an object we must feel it for some time.

There must be special nerve-endings which are capable of receiving heat impressions, because warmth applied to the nerve fibres themselves is not capable of giving rise to the sensation of heat. Thermic stimuli, no doubt, do affect nerve fibres, but only cause the sensation of pain when applied to them.

These nerve endings are not the same as those that receive touch and pressure impressions, because the appreciation of differences of temperature is not very delicately developed in the parts where the tactile sensations are most acute. Thus the cheeks and the eyelids are especially sensitive to changes of temperature, a fact known by people who want a ready gauge of the heat of a body, *e.g.*, a barber approaches the curling-tongs to his cheek to measure its temperature before applying it to the hair of his client. The middle of the chest is very sensitive to heat, while it is dull in feeling tactile impressions. The hand is far from being the best gauge of temperature, for heat appreciation is not developed in a due proportion to the keenness of its tactile sensibility. The larger the surface exposed to changes of temperature the more accurate the judgment at which we can arrive —the slightest changes being at once recognized when the entire surface of the body is exposed to them. The foregoing facts are well known to persons in the habit of testing the temperature of a warm bath without the aid of a thermometer ; they do not use the limited surface of a sensitive tactile finger-tip but plunge the entire arm into the water. The elbow, indeed, is the common test used by nurses in ascertaining that the water in which they are about to wash an infant is not too warm for that purpose.

Great extremes of heat or cold, such in fact as would act as stimuli to a nerve fibre, do not give rise to sensations of different temperatures, but simply excite feelings of pain. Thus, if we plunge our hand into a freezing mixture or into extremely hot water, it is difficult to say at once whether they are hot or cold—in both cases pain being the only sensation produced.

General Sensations.

We call general sensations those feelings, pleasurable or otherwise, which can be excited, without our being able to refer them to external objects, compare their sensation with those of the special senses, or even describe their exact mode of perception. Under this head are

enumerated Pain, Hunger, Thirst, Nausea, Giddiness, Shivering, Titillation, Fatigue, &c.

Of these only *pain* is commonly referred to any given part, and the attempt to localize pain with exactness soon shows how very different is our power in this respect, in the case of pain and in the case of tactile impressions. Thus when we strike our "funny-bone" (the ulnar nerve passing over the condyle of the humerus), by the tactile impressions of the skin we know the elbow is the injured part, but the locality of the pain is not so exactly to be determined, for it shoots down the arm to the little finger, and is indefinitely spread over the region to which the nerve is distributed.

In studying the laws which govern the perception of painful impressions we must make the experiments upon ourselves, since we alone can form conclusions from the sensations produced.

The best way to carry out experiments upon pain is to use extremes of temperature, as we can thus graduate the stimulation. The application of a liquid over 50° C., or below 2° C., causes pain. The suddenness of application to the part, and its duration, and the extent of surface, as well as the previous temperature, have important influence in the amount of pain produced.

The various kinds of pain with which we are all more or less familiar seem to be related in some way to their mode of production, but we are unable to assign any definite cause for these differences of character. Thus, though such terms as shooting, stabbing, burning, throbbing, boring, racking, dragging pain, are frequently used, and may be of diagnostic value, we have only an indistinct knowledge that throbbing depends on excessive vascular distension in a part, that sharp pains are produced by sudden excitation of a sensitive part, and the dull pains by the more permanent stimulation of a part less well supplied with nerves.

Further, pain, as we think of it, is a complex mental process, made up of many items, such as real sensory impressions, fear, disgust, &c. When a finger is to be lanced patients often cry out most loudly before they are touched with the knife, and show intense feeling when they look at the blood flowing from the wound.

Hunger and *thirst* are peculiar and indefinite sensations which are experienced when some time has elapsed since food or drink has been taken. The exact part of the nervous system in which these impressions arise has not been determined. They are, however, said to be associated with peculiar sensations in the stomach and throat respectively. In the same way the venereal appetite, though associated

with local sensations, cannot be referred to any one part of the nervous system.

Nausea is also a sensation which cannot be attributed to any part of the nervous centres. It commonly arises in response to afferent impulses, such as smells, sights, tastes, pharyngeal, gastric, or other visceral irritation, and is antagonistic to the appetites just named. All the sensations that give rise to, or precede nausea are associated in our minds with disagreeable impressions, and no doubt mental operations have much to do with its production. A child, free from affectation, may be heard to say of a castor-oil bottle which in itself is not ugly, "I can't bear to look at it, the very thought of it makes me feel sick."

Without any participation on the part of the mental functions, unavoidable nausea may come on from irregular movement, as that of a ship, which often causes nausea in those unaccustomed to the sea. Certain conditions of the blood flowing through the nerve centres also cause nausea, as when emetics are injected into the blood.

Giddiness, which consists of a feeling of inability to keep the normal balance, is often produced in connection with the last by irregular movements, but more surely by a rotatory motion of the body. Other afferent influences may give rise to it, viz., from the stomach, in some cases of irritation; from the eye, when we look from a height; from the semicircular canals of the ear by rotation of the body; and also from conditions of the blood, as in alcoholic toxæmia.

Shivering is the result of a peculiar nervous effect produced by afferent influences of an unpleasant kind, the sudden application of cold to the skin, a revolting sight, a shrill noise, or an intensely nasty taste—all excite a nervous condition which makes us shiver.

Titillation follows light stimulation of certain parts of the cutaneous surfaces. It is a peculiar general sensation, in moderation not disagreeable, and usually accompanied by a tendency to meaningless laughter and other reflex movements.

CHAPTER XXXI.

TASTE AND SMELL.

Sense of Taste.

Next to the sense of touch, which is unevenly distributed over the whole cutaneous surface, taste is anatomically the least accurately localised. Though confined to the mouth, its more accurate limitations are not easily fixed. The point, sides, and posterior part of the dorsum of the tongue can appreciate tastes; and probably parts of the palate also have the power, but in a much less degree. Indeed, though "the palate" is often spoken of as if it were the seat of taste, it really enjoys an insignificant share of this function compared with the tongue.

The power of being stimulated by various tastes is not restricted to the terminals of any one nerve, but is shared by some of those of at least three trunks, which also transmit impulses arising from other forms of stimulation. The glosso-pharyngeal division of the 8th pair sends branches to the posterior part of the tongue, which are no doubt connected with the special taste organs. The lingual branches of the 5th—commonly called the gustatory nerves—have also terminals capable of being excited by taste, and probably some fibres of the chorda tympani are employed in this function.

In the furrows around the circumvallate papillæ, and also, but more sparsely, on the sides of the fungiform papillæ of the tongue, are found peculiar organs called "taste-buds" or "taste-goblets." They are embedded in the stratified epithelium, with the cells of which their outer layers are intimately connected. They are flask-shaped bodies, composed of concentric series of modified epithelium cells arranged like the staves of a barrel, pinched together at the base and at the free surface, where they closely surround the projecting points of the central elements. These consist of nucleated bars, supposed to be the nerve terminals. The whole arrangement reminds one somewhat of the construction of the head of a ripe artichoke.

Nerves can be seen entering these bodies, and are in all probability directly connected with the modified epithelial cells of which they

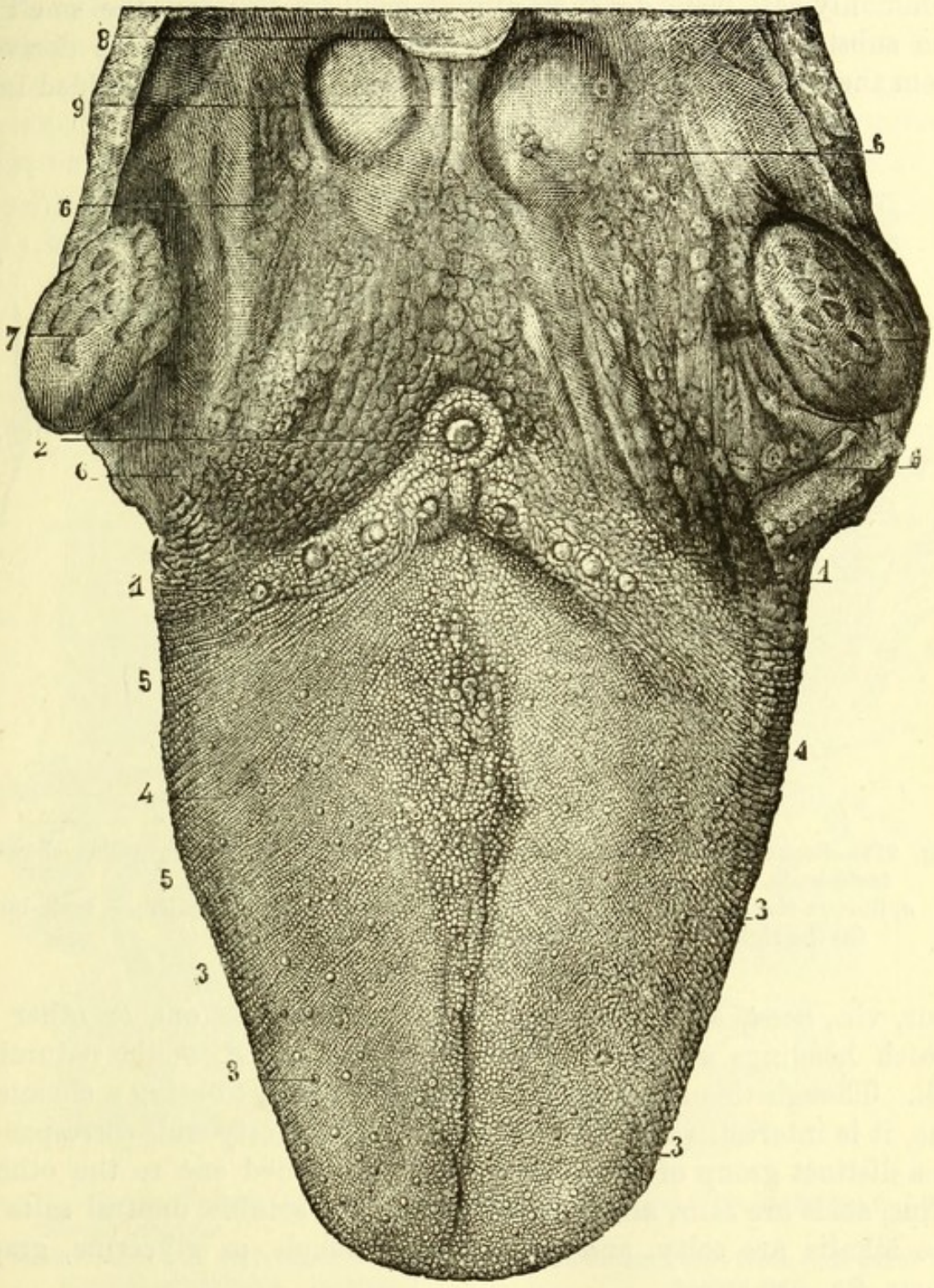


Fig. 212.—Drawing of upper surface of the tongue, showing the position of the papillæ. 1 and 2, Circumvallate papillæ. 3. Fungiform papillæ. 4. Filiform papillæ. (Sappey.)

are made up. The relation of the glosso-pharyngeal nerves to these taste-buds has been shown by the fact that in the rabbit (in which animal they are crowded together in a special organ so as to be

easily found) they degenerate, and in a few months disappear, after one of these nerves has been cut.

The genuine taste sensations are very few. Much of what we commonly call taste depends almost exclusively upon the smell of the substance, and we habitually confuse the impressions derived from these two senses.* The different tastes have been divided into

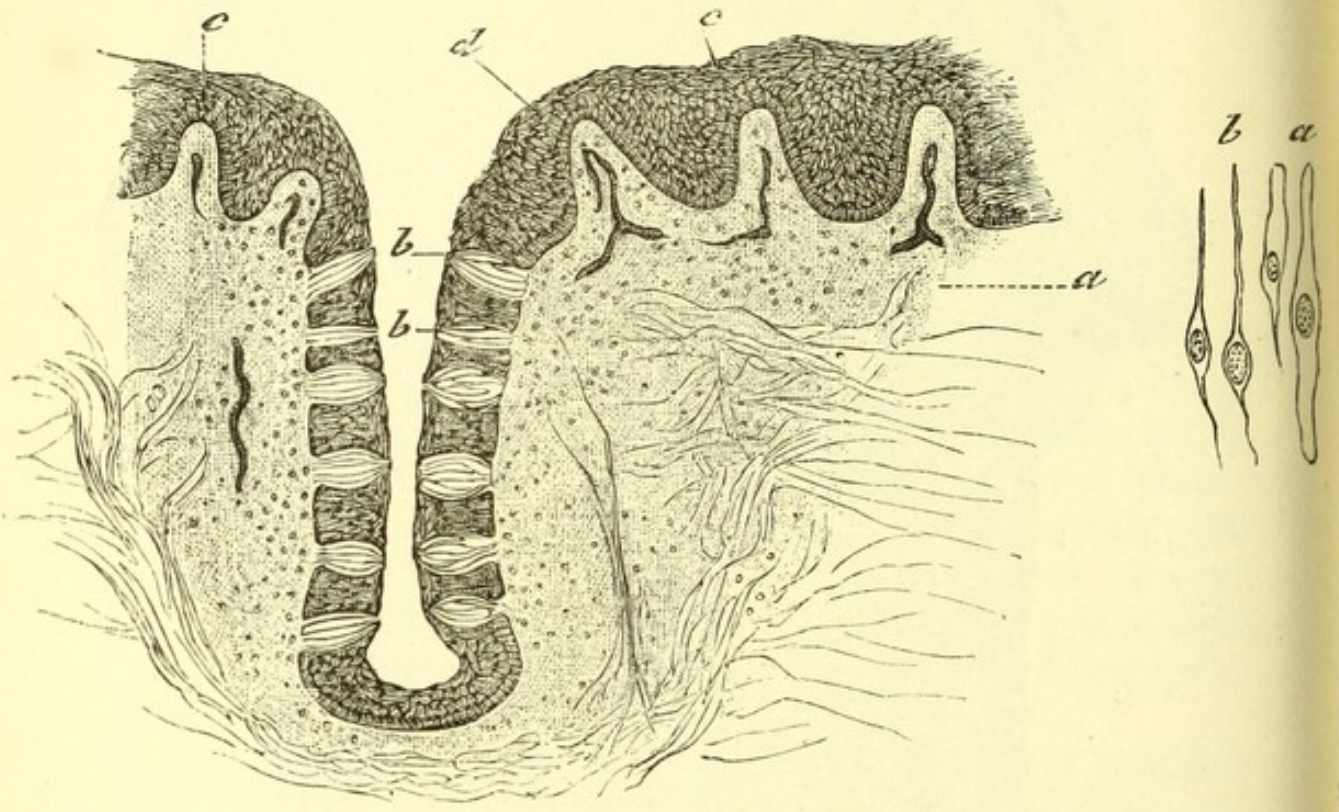


Fig. 213.—Section through depression between two circumvallate papillæ, showing taste-buds. (Cadiat.)
a, fibrous tissue of papilla; *d* and *c*, epithelial covering of papilla; *b*, taste-buds. On the right *a*, *b*, show the separate cells of a taste-bud.

four, viz., *sweet*, *sour*, *bitter*, *and salty*, under some one or other of which headings all our tastes, properly so called, would naturally fall. Though this classification has no just claim to being a chemical one, it is interesting to know that each taste pretty well corresponds to a distinct group of substances chemically allied one to the other. Thus, acids are sour, alkaloids are bitter, the soluble neutral salts of the alkalis are salty, and polyatomic alcohols, as glycerine, grape sugar, &c., are sweet.

These substances probably act on the nerve terminals as chemical

* Many of the comestibles, the taste of which we most prize, have really no taste, but only a smell which we habitually confound with taste, having mingled the experience obtained from the two senses. Thus, if the draft of air be carefully excluded from the nose, wine, onion, &c., may easily be proved to have no taste. Hence the familiar rule of holding the nose adopted in taking medicine with a nasty "taste."

stimuli, because they must be in solution to be appreciated. If solid particles be placed on the tongue they must be dissolved in the mouth fluid before they can excite the taste organs.

In order to explain the appreciation of the different tastes we may imagine that there are different kinds of terminals, each of which is or is not influenced by various substances as they possess a special sweet, sour, bitter, or salt energy. From these different terminals pass fibres bearing impulses to certain central cells, each of which is capable of exciting a sweet, sour, bitter, or salty sensation, as the case may be.

Sense of Smell.

The numerous delicate nerves which pass from the olfactory bulb to the mucous membrane of the upper and part of the middle meatus

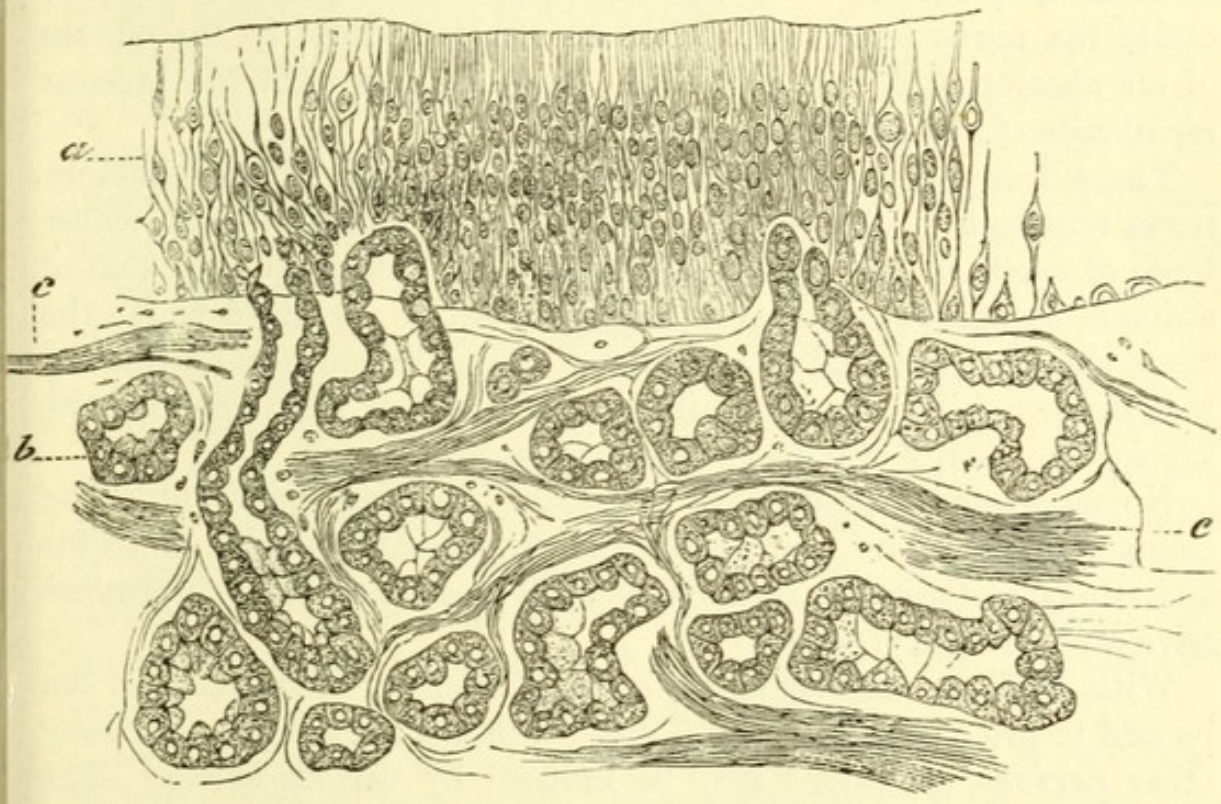


Fig. 214.—Section through the mucous membrane of the nasal fossa in the level of the olfactive region.
a, Epithelial cells and bundles of nerves; *b*, Glands separated from each other by bundles of nerves, *c*. (Cadiat.)

of the nose form the special nerves of smell. When certain subtle particles we call odours come in contact with the terminals of these nerves they excite impulses which, on arriving in the special centres of the brain, give rise to the impressions of smell.

Anatomically the relations of the olfactory region are well defined. Its mucous membrane is not covered with motile cilia, as is that of the rest of the nasal cavity, and it is less vascular and peculiarly pigmented, looking yellow to the naked eye when compared with the neighbouring membrane. The epithelial cells are elongated into peculiar cylinders, between which lie long thin rods, ending on the surface in free hair-like processes. The deeper extremities of these rod-shaped filaments expand to surround a nucleus, and are then continued into a network of filaments, into which prolongations of the epithelial cells also seem to pass, and in which the delicate fibrils of the olfactory nerve can be traced. The existence of direct communication between the nerves and the rod-shaped filaments and the epithelial cells is satisfactorily established in some animals.

The odorous particles must be in the form of gases, in order to be carried by the air into the olfactory region, and the air must be kept in motion, by sniffing it in and out of the nasal cavity, in order to excite the nerve terminals, which are not influenced by the odours of air absolutely at rest, though it be in contact with the mucous membrane of the olfactory tract.

The extreme delicacy of appreciation of odours by the olfactory nerve terminals is very remarkable. Even in human beings, whose sense of smell is but poorly developed when compared with that of animals, an amount of odorous substance can be perceived which the finest chemical tests fail to appreciate. Thus Valentin has estimated that the two-millionth of a milligram of musk is sufficient to excite the specific energy of a man's olfactory apparatus.

No satisfactory classification of odours has been made out. The common division into agreeable and disagreeable smells, or scents and stinks, is dissimilar in different individuals, and therefore cannot have a physiological basis.

With smell, as with taste, no degree of intensity of stimulation can be said to produce pain, though disgust, nausea, vomiting, and many other nervous operations may be induced by various smells. The appetites are either excited or annulled by different excitations of the olfactory nerves.

CHAPTER XXXII.

VISION.

NEXT in importance to those impulses which we receive from the skin are those conveyed to the brain from the outer world by the second pair of cranial, or the optic nerves.

The ending of the optic nerve differs from any of those met with in the skin, by being enclosed in a very specially arranged organ —the eyeball—an apparatus for bending the rays of light, so that they exactly reach the delicate sheet of complicated nerve-ending which is here spread out. Only the blood and other tissues of the eye come in contact with the endings of the optic nerve, which are thus placed out of the way of ordinary nerve stimulation.

Further, the light, of which the optic nerves convey intelligence to the brain, is not properly a nerve stimulus, being merely the waving of an imponderable medium, the existence of which is assumed. Besides the special arrangements in the eyeball for bringing the rays of light to bear on the nerve-endings, there must here be some extremely sensitive arrangement by which the ether-waves, which we call light, can be converted into a nerve stimulus, or in some way made to affect the nerve terminals in the retina.

By means of the sense of sight we obtain knowledge of objects at a distance from us, because all these objects reflect more or less light, and thus make different impressions upon the terminals of the optic nerve forming the outer layer of the retina.

Light, then, is the *adequate stimulus* for the retinal nerve-endings, and the impulse caused by light is the only impression the optic nerve is in the habit of carrying to our sensoria, where the sensation of light is formed and distributed among the cells of the brain so as to enable us to come to visual judgments and conclusions. As already mentioned, no matter what stimulus, electric, mechanical, or other

be applied to the fibres of the optic nerve, the sensation produced is simply light, and this is thought of as if it came through the eye from the outer world.

The study of the function of vision may be divided into:

1. The path the light takes on its way through the eye to reach the retina.

2. The molecular changes in the retina which give rise to stimulation of the optic nerves.

3. The sensations arising in the sensorium as the result of the molecular changes set up in the cerebral nerve cells by the impulses from the optic nerve.

4. The visual perceptions and judgments which our consciousness is capable of elaborating from the visual sensations.

The Tunics of the Eyeball.

The organ of vision of vertebrate animals is enclosed in a firm case of fibrous tissue called the *sclerotic coat*, which is continuous with the sheath of the optic nerve. It is seen between the eyelids under the transparent conjunctiva, and known as the white of the eye. It gives shape and protection to the eye, and though translucent, is not transparent. In front a round window-like portion, called the *cornea*, forms the anterior segment of this protecting covering of the eyeball. The cornea is distinguished from the sclerotic not only by its glass-like transparency, but also by being part of a lesser sphere than the sclerotic, and thus projecting a little more than the rest of the bulb.

Closely attached to the inside surface of the sclerotic is a soft, thin, black vascular sheet of tissue called the *choroid coat*, which supplies the eyeball with blood. It is made up chiefly of blood-vessels and stellate, pigmented, connective tissue cells. Its outer layer is traversed by arteries and veins of relatively large size, and its inner layer is composed of a dense network of close-meshed capillary vessels. As the cornea region is approached, the choroid is peculiarly modified and thrown into folds, called *ciliary processes*, forming a series of vascular folds, radiating from the margin of the cornea. At the edge of the cornea the choroid is more firmly attached to the sclerotic by a circular muscle (*ciliary muscle*), and also by bands of tissue from the posterior surface of the cornea which hold it in position; the fibres of the ciliary muscle, running under the ciliary processes,

radiate from the margin of the cornea towards the choroid, to which they are attached. In a modified form, known as the *iris*, this vascular and pigmented coat of the eye leaves the sclerotic, and hangs freely in a fluid, being recognised through the clear cornea as

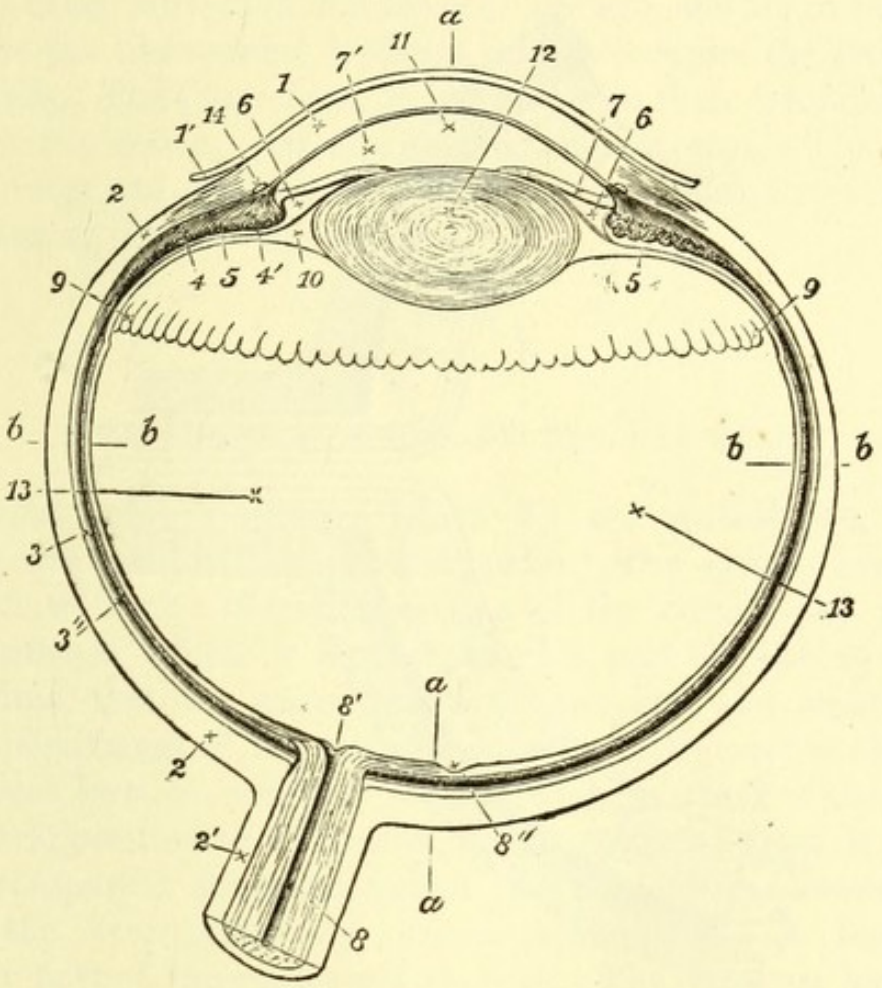


Fig. 215.—Diagram of a horizontal section through the human eye.

1. Cornea; 1'. Conjunctiva; 2. Sclerotic; 3. Choroid; 4. Ciliary processes; 4'. Ciliary muscle; 5. Suspensory ligament of lens; 6. So-called posterior chamber, between the iris and the lens; 7. Iris; 7'. Anterior chamber in front of the iris; 8. Optic nerve; 8'. Entrance of central artery of the retina; 8''. Central depression of retina or yellow spot; 9. Anterior limit of the retina; 10. Canal of Petit in front of the hyaloid membrane; 11. Aqueous chamber; 12. Crystalline lens; 13. Vitreous humour; 14. Circular venous sinus which lies around the cornea; a—a, anterior-posterior, and, b—b, transverse axis of bulb.

a coloured circular curtain, attached to the inside of the periphery of the cornea, having a central aperture, which looks black, and is familiarly known as the *pupil*. The pupil is merely an opening in the iris, which allows the rays of light to pass into the interior of the eyeball.

Besides supplying nutrition to the non-vascular central parts of

the eyeball, the choroid is useful in vision by preventing the reflection of the light from the background of the eye in such a way as would cause irregularity of its distribution, and thus dazzle and interfere with the distinctness of the image. The choroid is elastic, and can move over the neighbouring sclerotic; it can be drawn

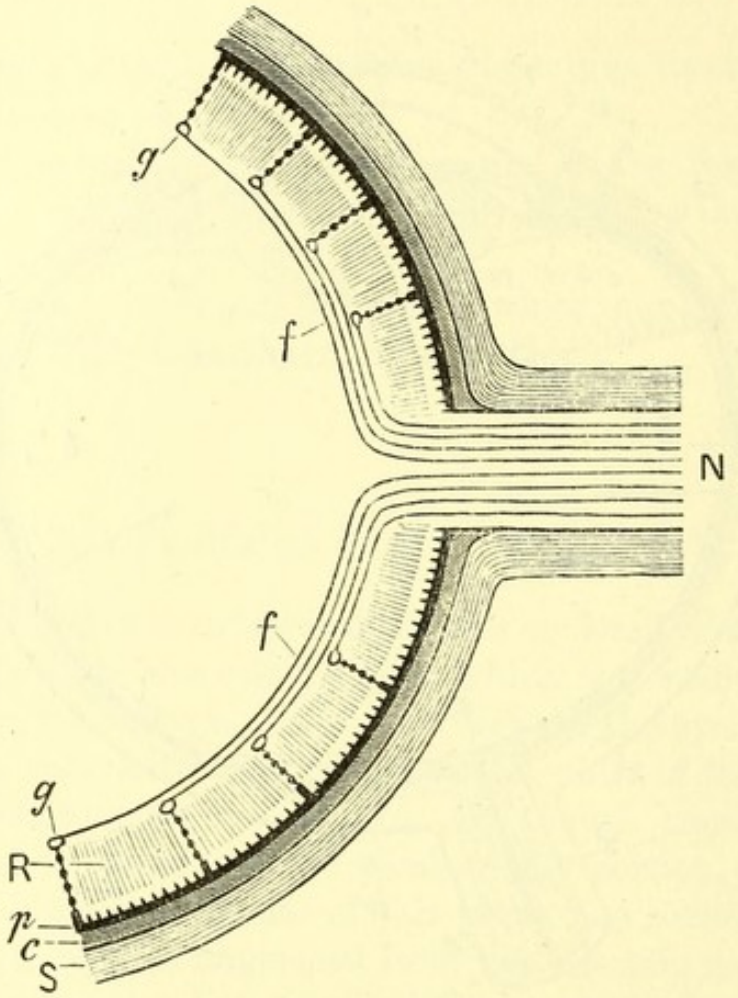


Fig. 216.—Showing the course of the fibres of the optic nerve, N, as they pass along the inner surface of retina R, to meet the ganglion cells *g*, whence special communications pass outwards to the layer of rods and cones in the pigment layer *p*, next the choroid *c*, within the sclerotic S.

forwards by the contraction of the radiating ciliary muscle, which acts as a tensor of the choroid membrane.

The iris has a special power of motion, by means of which the opening in it can be made smaller, so as to regulate the amount of light admitted to the eye, and cut off more or less of the rays which would pass through the margin of the dioptric media. The importance of this will be better understood further on.

Within the choroid coat, and in immediate contact with it, is the nervous coat, or *retina*, formed by the expansion of the optic nerve,

which passes towards the sclerotic obliquely, and enters it somewhat to the nasal side of the axis of the eye. The retina lines all the back part of the eyeball, and stretching forwards, becomes fused with the ciliary processes, where, however, the nervous elements of the coat are wanting. The fibrils of the optic nerve reach the inner surface of the coats of the eye, and lie in immediate relation to the transparent medium, which occupies the greater part of the bulb. The fibres then lie internally to their terminals, which turn outwards and are set against the choroid coat. The ultimate nerve-endings are situated in pigmented protoplasmic cells, which form the outer layer of the retina.

The Dioptric Media of the Eye-ball.

The transparent substances which fill the eyeball are, together with the *cornea*, called the dioptric media. The *aqueous humour* lies in contact with the posterior surface of the cornea, and just fills the prominence which is formed by this part of the eye. It is in this fluid that the movable iris is stretched and separates the aqueous department of the eye into anterior and posterior chambers. The *vitreous humour* occupies much the larger share of the eyeball. It lies in apposition to the retina, being separated from it only by a thin transparent structure, called the *hyaloid membrane*, which encloses the clear gelatinous vitreous humour, and is fused with the ciliary part of the retina and choroid. The vitreous humour is developed from the young connective tissue of the mesoblast, and we find in the adult that mucus is the most abundant chemical substance in its texture, though the branched cells of the original mucous tissue have nearly all disappeared.

The most important of the dioptric media is the *crystalline lens*. It is placed between the aqueous and the vitreous humours, just behind the iris, which lies in contact with its anterior surface. It is like a strong magnifying glass, bi-convex in shape, the posterior surface being more convex than the anterior. The lens is much harder than the vitreous humour, but its outer layers are little denser than a stiff jelly. It is enclosed by a firm elastic capsule, which is drawn tightly over the anterior surface, and influences its shape. The lens is held in its position by the *suspensory ligament*, a thickened part of the hyaloid membrane, which is continued forwards and attached to the anterior surface of the capsule, near its margin. The lens and

its capsule, together with the vitreous humour, may be said to be enclosed in the hyaloid membrane, which, in front, is thickened and attached to the ciliary part of the choroid and the capsule. Thus any tension exercised by the suspensory ligament tends to tighten the anterior part of the capsule, and flatten the anterior surface of the lens.

The shape of the lens varies at different times of life, being nearly spherical in the infant and tending to become less convex in old age

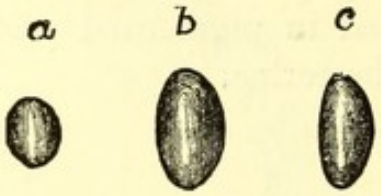


Fig. 217.—Diagram of lens viewed from the side at different periods of life. *a*, at birth; *b*, Adult; *c*, Old age. (Allen Thomson.)

(Fig. 217). The lens is developed from the outer layer of the embryo by the gradual thickening and growing inwards of the epithelium, which meets the optic cup, and after a time is cut off

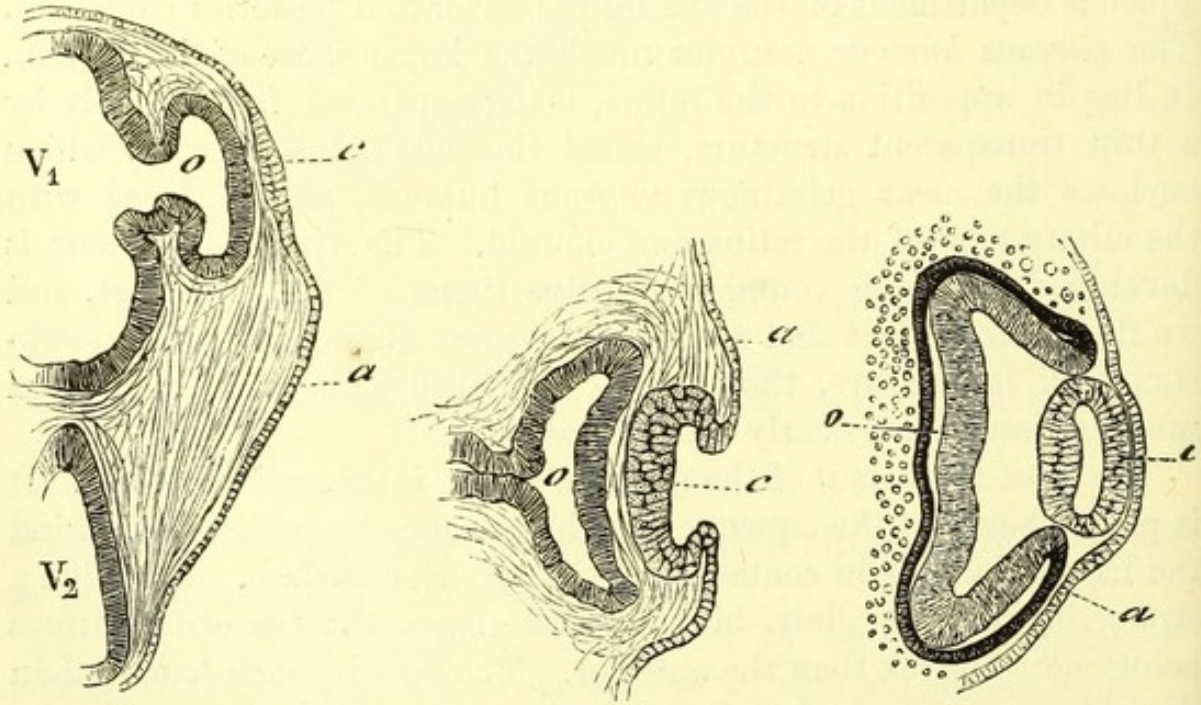


Fig. 218.—Showing early stages of the development of the lens. *c*, Epithelial tissue about to form the lens; *o*, Optic cup; *a*, Epidermis. (Cadiat.)

from the parent tissue. The stages of its development may be followed in the accompanying woodcuts (Fig. 218).

The lens is composed of a number of peculiar band-like cells, derived from the epithelium. These are cemented together in parallel rows, eccentrically arranged in layers. These bands are hexagonal in transverse section, and in the younger periods of life may be seen to contain nuclei.

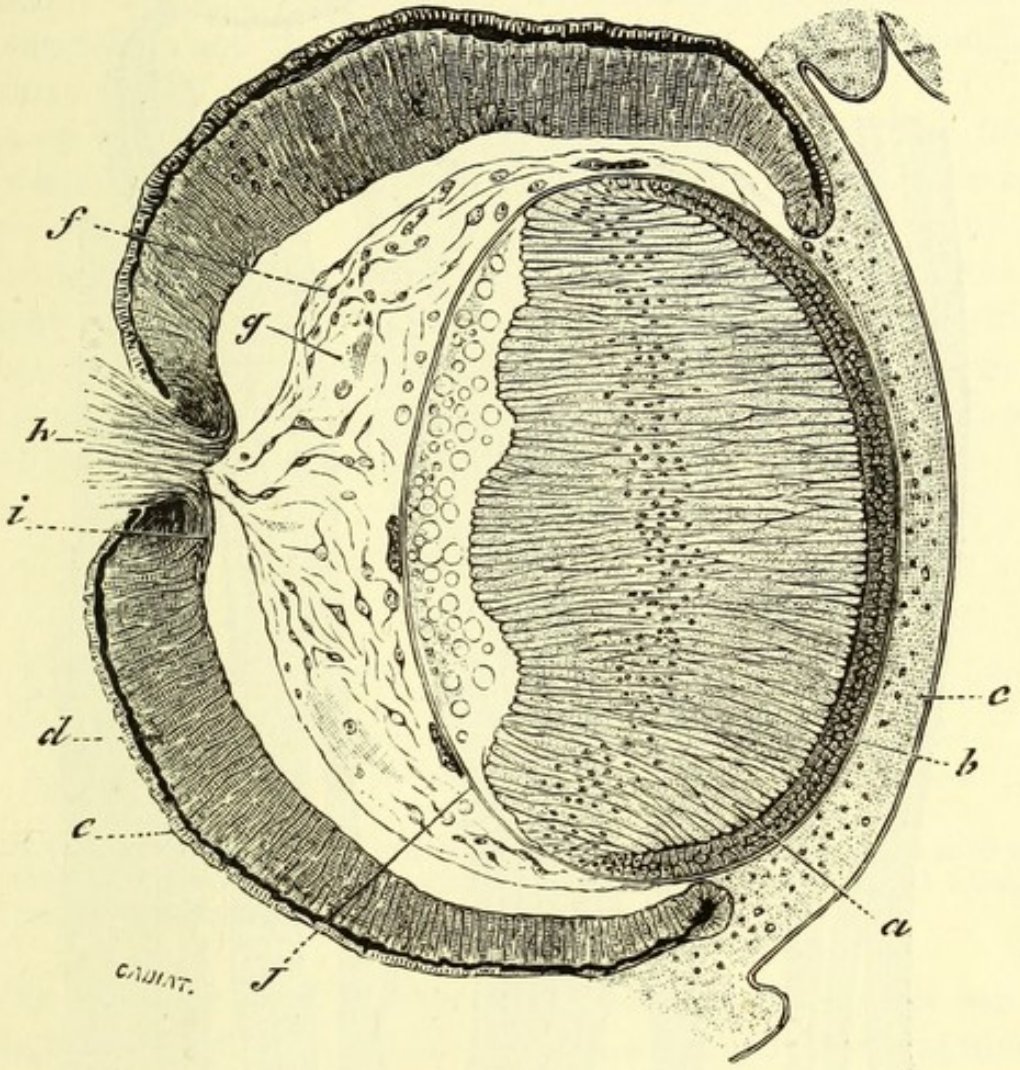


Fig. 219.—A further stage of the development of the lens. (Cadiat.)

a, Elongating epithelial cells forming lens; *b*, Capsule; *c*, Cutaneous tissue becoming conjunctiva; *d*, *e*, Two layers of optic cup forming retina; *f*, Cell of mucous tissue of the vitreous humour; *g*, Intercellular substance; *h*, Developing optic nerve.

In the living state the lens is perfectly transparent, but after death it becomes slightly opaque. The nutriment for the adult lens is derived from the vessels of the choroid, which, however, do not come into direct communication with its texture. On this account he nutrition of the lens is not so perfect as that of many other

tissues, and is but imperfectly repaired after injury, which always leaves more or less opacity. Even without injury, opacity, giving rise to cataract, sometimes occurs during life.

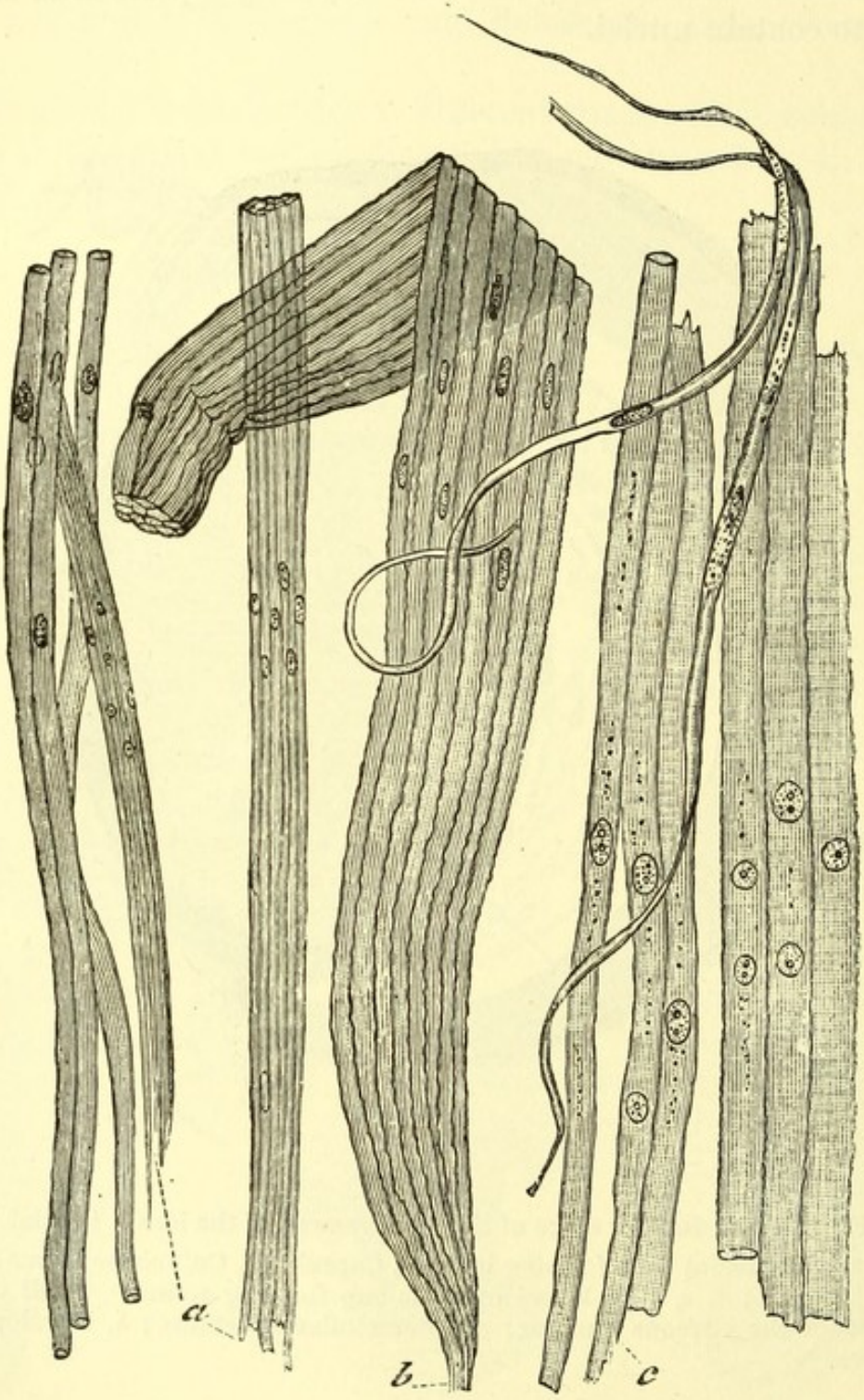


Fig. 220.—Fragment of lens teazed out to show the separate fibres. (Cadiat.)
a, *b*, and *c*, show fibres with different sized nuclei.

Chemically, the lens is made up of globulin, and furnishes a ready source for obtaining this form of albumin for examination.

Dioptrics of the Eye.

Light travels through any even transparent body, such as the atmosphere, in a straight line. But when it meets any change in density, particularly when it has to pass obliquely into a denser medium, the ray is bent so as to run in a direction more perpendicular to the surface of the denser body. The degree of bending or *refraction* of the rays depends on the difference in optical density of the two media and the angle at which the ray strikes the surface of the more dense.

On its way to the sensitive retina, the light has to pass through the various transparent media just named, viz., the cornea, the aqueous humour, the crystalline lens, and the vitreous humour. On entering these media, which have different densities, the rays of light emitted by any luminous body become bent or refracted, so that they are brought to a focus on the retina, just in the same way as parallel rays of light from the sun may be focussed on a near object by means of an ordinary convex lens.

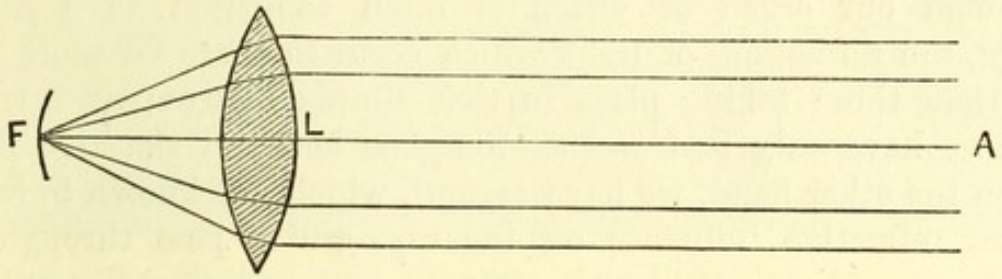


Fig. 221.—Diagram showing the course of parallel rays of light from A, in their passage through a biconvex lens L, in which they are so refracted as to bend towards and come to a focus at a point F.

Only so much light reaches the fundus of the eye as can pass through the opening in the iris, so that a comparatively narrow and

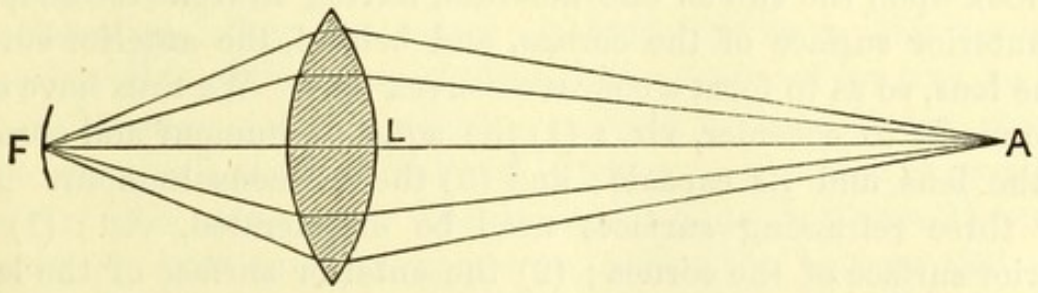


Fig. 222.—Diagram showing the course of diverging rays, which are bent to a point further from the lens than the parallel rays in last fig.

varying beam is admitted to the chamber in which the nerve-endings are spread out for its reception.

If we hold a biconvex lens at a certain distance from the eye and look out of the window through it, we see an inverted image of the landscape. If we place a piece of transparent paper behind the lens, we can throw a representation of the picture on it, which will be seen to be inverted. This power of convex lenses is employed in the instrument used for taking photographs called a *camera*, which consists of a box or chamber into which the light is allowed to pass through a convex lens, so that an inverted image of the objects before it is thrown upon a screen of ground glass within the box. When the sensitive plate replaces the screen, the light coming through the lens makes a photograph.

Just in the same way an inverted image of the things we look at is thrown on the retina by the refracting media of the eye. This may be seen in a dark room, if a candle be placed at a suitable distance in front of the cornea of an eye taken from a recently-killed white rabbit. When cleared of fat and other opaque tissues, the sclerotic is transparent enough to act as a screen upon which the inverted candle flame can be recognised.

Though our organ of vision is often compared to a *camera obscura*, the refractions of light which occur in it are far more complex than those taking place in that simple instrument. In the latter we have only two media—the glass lens and the air; in the eye, on the other hand, we have several, which are known to have a distinct refractive influence on the rays which pass through the pupil.

Three Media and Refracting Surfaces.

Since the surfaces of the cornea, however, are practically parallel, we may neglect the difference between it and the aqueous humour, and look upon the two as one medium, having in front the shape of the anterior surface of the cornea, and behind, the anterior surface of the lens, so as to form a concavo-convex lens. We thus have only three media to consider, viz.: (1) the aqueous humour and cornea; (2) the lens and its capsule; and (3) the vitreous humour. And only three refracting surfaces need be enumerated, viz.: (1) the anterior surface of the cornea; (2) the anterior surface of the lens; and (3) the posterior surface of the lens.

These refracting surfaces may all be looked upon as portions of spheres whose centres lie in the same right line, and hence may be said to have a common axis. The eye may be regarded as an optical system, centred round an axis which passes through the middle

point of the cornea in front, and the central depression (fovea centralis) of the retina behind. This is spoken of as the optic axis of the eye.

The rays of light entering the eye are most strongly refracted at the surface of the cornea, because they have to pass from the rare medium, the air, to the denser cornea and aqueous humour. So also more bending of the rays occurs between the aqueous humour and the anterior surface of the lens than between the posterior surface of the lens and the vitreous humour.

The lens is not of the same density throughout, but denser in the centre, and being made up of layers, the central part refracts more than the outer layers.

The manner in which the *inversion of the image* is produced by a convex lens, is shown in the accompanying figure, in which the lines

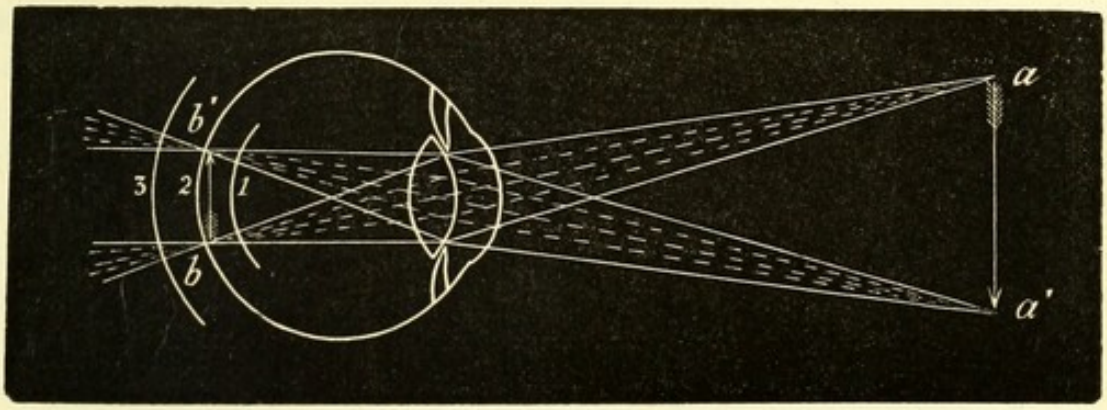


Fig. 223.—Showing the course of the rays of light from two luminous points to the retina. The rays from the point *a* on passing through the cornea, lens, &c., are collected on the retina at *b*. Those from *a'* meet at *b'*, and thus the lower point becomes the upper.

correspond to the rays passing from two points through the lens. If the arrow *a a'* be taken for the object, from either extremity of it rays pass through, and are more or less bent by the lens. It will be sufficient to follow the course of three rays from the head of the arrow. One of these passes through the centre of the lens, and leaves it in the same direction which it entered, because the two surfaces at the points where it entered and left may be regarded as parallel, and so cause no refraction. The rays which do not pass through the centre are bent on entering and on leaving the lens, so that they all meet at the same point and there produce an image of the head of the arrow, at *b'*. In the same way the feather end of the arrow is produced at *b* ; the position of the image of the object is thus reversed by the light rays passing through the lens.

In a biconvex lens, with two surfaces of the same degree of

convexity, the central point through which the rays pass without being refracted is easily made out, as it is the geometrical centre of the lens. This central point is spoken of as the optical centre. With systems of lenses of varying convexity, and of more than one in number, as we have in the eye, where the rays of light are bent at different surfaces, it is much more difficult to determine the optical centre. However, by means of the measurements made by Listing, two points close together are known, which may be said to correspond practically with the optical centres of the eye ; they lie in the lens, between its centre and posterior surface. The path of the various rays may thus be exactly made out.*

The rays which come from a distant luminous point and fall upon the eye, are refracted by the cornea and aqueous humour, so as to be made *convergent* on their way to the lens ; they are then further bent at the surfaces of the lens, so that they are brought exactly to a point on the retina. That is to say, for distant luminous points, the retina lies exactly in the plane of focus of the dioptric media of the normal eye.

This convergence of the rays to a point on the retina, is the first essential for seeing clear and distinct images ; for if the rays from each point of a luminous body were not united on the retina as points, the effects of the different rays from the various points of a body would become mixed, and there would be loss of definition of its image.

The rays from any bright point which enter the eye through the pupil may be imagined to form a luminous cone, the point of which lies at the retina, and its base at the pupil. After their union at the point of the cone, the rays would diverge again if the retina were not there to receive them.

Scheiner's Experiment.

It may be seen from the foregoing figure that if the retina, which normally would lie at 2, were placed nearer the dioptric apparatus, say at 1, or further from it, at 3, it would not meet the exact point of the luminous cone, but would receive the rays either before they came to a point, or after they had diverged from it. Thus indistinct

* The impossibility of making clear the important relationships, such as nodal points, and other constants of the eye in a short text-book, and the deterrent effect exerted upon the mind of a junior student by brief incomprehensible statements, have induced the author to omit this part of the subject. He must refer those who are anxious to learn the cardinal points of the eye, to the more advanced text-books.

rings of light would be seen instead of one luminous point, and an image would be blurred and indefinite.

From this it follows that the eye, when quite passive, can only get an exact image of bodies which are placed at a certain distance from it, just as, for any given state of a camera, only those bodies in one plane come into focus and give a clear picture on the screen. If the dioptric apparatus of the eye were rigid and unalterable, since the relation of the retina to it is permanently the same, we could only see those objects clearly which are at a given distance from the eye. We know, however, that we see as distinct an image of distant as of near objects, and we can look through the window at a distant tree, or can adjust our eyes so as to see a fly walking on the window pane. We cannot see both distinctly at the same moment. This power of focussing may be demonstrated by what is known as Scheiner's experiment, which is carried out in the following way.

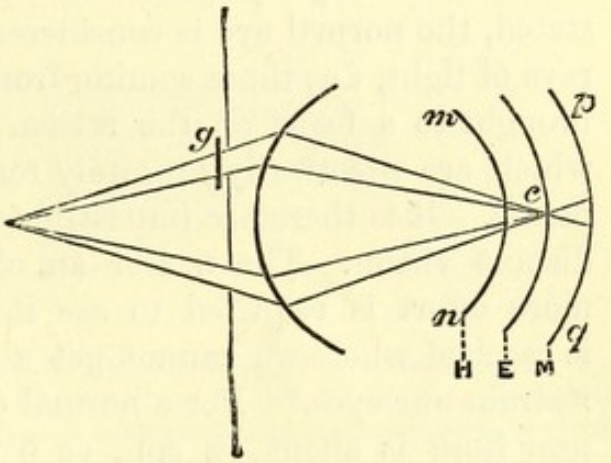


Fig. 224.—To illustrate Scheiner's experiment; for explanation, see text.

Two pinholes are made in a card at a distance from each other not wider than the diameter of the pupil. The card is then brought close to the eye, so that a small object —such as the head of a bright pin—can be seen through the holes. The dioptric media being fixed, moving the object nearer to or further from the eye would have the same effect as changing the relation of the retina to *m n* or *p q* in fig. 224, by means of which we may explain the following observations: (1) The eye being fixed upon the object (of which only one image is seen), move the pin rapidly away; two objects now appear, showing that the rays coming through the holes have met before they reach the retina as at *p q*. (2) Move the pin near the eye; again two very blurred objects are seen, for the rays have not met when they strike the retina, as at *m n*. (3) Keeping the object in the same position, alter the gaze, as if to look first at distant and then at near objects; in both extremes two images are seen. (4) When the object is in exact focus as at *c*, the closure of one of the holes does not affect the single image. (5) When two images are seen, closing the right hand hole at *g* causes the right or left image to disappear according as the focus *c* falls short of *m n* or is

beyond *p q*, the retina. (6) By moving the pin's-head nearer the eye, a point is reached at which the object cannot be brought to a focus as a single image. This limit of near accommodation marks the near point. A little attention teaches us that looking at the near object requires an effort which looking at the distant one does not; in fact, we have to do something to see things near us distinctly. This act is the voluntary adjustment of the eye which we call its accommodation for near vision.

Accommodation.

The difference of distance for which we can adjust our eyes is great, so that our *range of distinct vision* is very extensive. As already stated, the normal eye is considered to be constructed so that parallel rays of light, *i.e.*, those coming from practically infinite distance, are brought to a focus on the retina. This is why we see the stars—which are practically infinitely remote from us—as mere luminous points. It is therefore impossible to fix a *far limit* to our power of distant vision. The nearer an object is brought to our eyes, the more effort is required to see it distinctly, until at last a point is reached where we cannot get a clear outline, no matter how we "strain our eyes." For a normal eye, called the *emmetropic eye*, this *near limit* is about 12 cm., or 5 inches, but it varies in different individuals.

For objects that are over 10 metres distance very little change in the eye is required to see each distinctly, and the nearer the object approaches the more frequently the adjustment of the eye has to be altered to see it clearly. When the eye is focussed for any point within the limits of distinct vision a certain range of objects at different distances from the eye can be recognised without moving the adjustment. The range of this power is measured on the line of vision, and called the *focal depth*. In the distance we can take in a great depth of landscape, without effort or fatigue; but when looking at near objects the focal depth is less, and we must constantly accommodate our eyes afresh in order to see clearly objects at slightly different distances because of the shallowness of the focal depth in the nearer parts of visual distance.

The *method* by which the accommodation of the eye is effected differs from anything that can be applied to an artificial optical instrument, and is more perfect.

The following alterations are observed to occur in the eye during active accommodation, *i.e.*, when looking at near objects. (1) The

iris contracts so that the pupil becomes smaller; (2) the central part of the anterior surface of the crystalline lens moves slightly forwards, pushing before it the pupillary margin of the iris, so that the lens becomes more convex; (3) the posterior surface of the lens also becomes more convex owing to the general change of shape of the lens, but the centre of this surface does not change its position; (4) both eyes converge.

These changes can be seen in the accompanying diagram, showing a section of the lens, cornea, and ciliary region (Fig. 225), in the left-

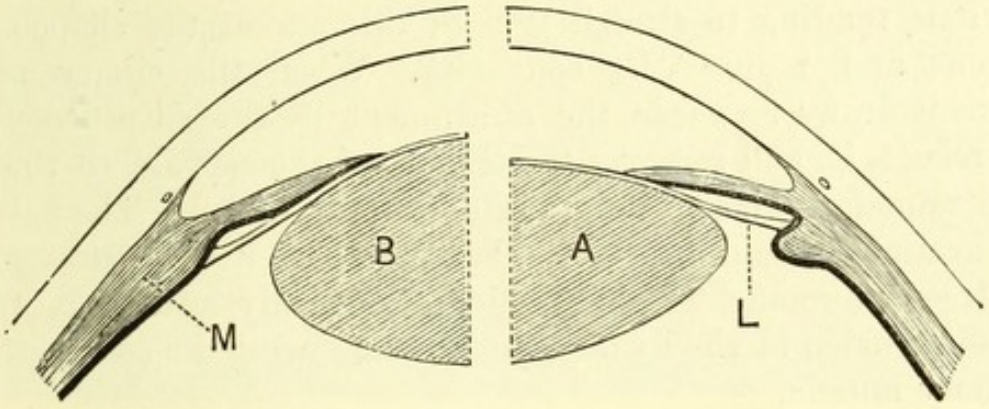


Fig. 225.—Diagram showing the changes in the lens during accommodation. The muscle on the right is supposed to be passive as in looking at distant objects, the ligament (L) is therefore tight, and compresses the anterior surface of the lens (A) so as to flatten it. On the left the ciliary muscle (M) is contracting so as to relax the ligament, which allows the lens to become more convex. This contraction occurs when looking at near objects.

hand side of which the lens is drawn in the position it assumes when accommodated for near objects. These movements can be seen in life by observing the changes in relative positions, &c., of the reflections of a candle flame thrown from the cornea and the two surfaces of the lens. On the cornea is seen a bright upright flame; next comes a large diffused reflection from the anterior surface of the lens, and at the other side of this a small inverted image of the flame reflected from the posterior surface of the lens. When the adjustment is changed by looking from a far to a near object, the image on the front of the lens becomes smaller and moves towards the centre of the pupil. The image on the back of the lens also becomes smaller but does not change its position. The amount of movement has been accurately measured by a special instrument called an *ophthalmometer*. The motions can be more exactly studied by means of the *phakoscope*, a dark box, in which prisms are placed before the observed eye, and each image is made double. The change

in relative position of the two is more readily recognised than a mere change of size of the one.

Muscular mechanism of accommodation.—The alteration in the shape of the lens is accomplished by the action of the muscular layer already named, which radiates from the edge of the cornea to the ciliary region of the choroid coat, where it is attached. When the ciliary muscle contracts it draws the choroid coat and the connections of the suspensory ligament of the lens slightly forwards, the junction of the cornea and sclerotic being its fixed point. Under ordinary circumstances, the eye being at rest, the suspensory ligament is tense and exerts a radial traction on the anterior part of the capsule of the lens, tending to stretch it flat; this affects the shape of the soft lens and reduces its convexity. When the ciliary muscle shortens it draws forwards the attachment of the suspensory ligament, relaxes it, and removes the tension of the capsule, so that the unconstrained elastic lens bulges into its natural form. The posterior surface cannot extend backwards, because there it is in contact with the vitreous humour, which is held more firmly against it by the increased tension of the hyaloid membrane during the contraction of the ciliary muscle.

Some circular muscular fibres help to relax the ligament and relieve it from the increased pressure which the contraction of the radiating fibres must indirectly cause on the vitreous humour.

The act of accommodation is a voluntary one, the nerve bearing the impulse to the ciliary and iris muscles, coming from the 3rd nerve by the ciliary branches of the lenticular ganglion. The local application of the alkaloid of the belladonna plant (atropin) causes paralysis of the ciliary muscle and wide dilatation of the pupil; and the alkaloid of the Calabar bean (physostigmin) produces contraction of the muscle of accommodation and extreme contraction of the pupil.

Defects of Accommodation.

Myopia.—It has been said that the "near limit" of distinct vision differs in many persons from the twelve centimeters of the normal emmetropic eye, and it is found that the power of accommodation varies very much in different individuals. Thus in "short sighted" people, who have *myopic* eyes, *i.e.*, in which parallel rays are focussed short of the retina, the near limit may only be half the normal, *i.e.*, five centimeters, and the far limit, which is normally indefinite, is found to be within a comparatively short distance of the eye. They,

therefore, cannot see distant objects clearly, since the rays are focussed before the retina is reached, and then diverging, cause diffusion circles and a blurred picture. The work of their accommodation is also much more laborious, since they can only see in that part of the range of accommodation where the adjustment has to be altered for slight variations of distance. The defect can be made much less distressing by the use of concave glasses, which make parallel rays strike the cornea as divergent ones, and thus allow them to be focussed on the retina.

Hypermetropia.—Another abnormality is "long sight." In the

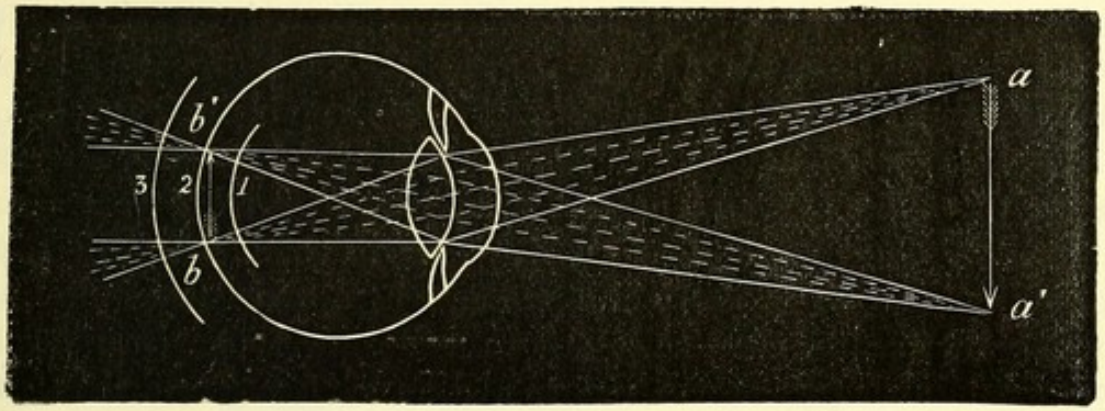


Fig. 226.—Showing the course of the rays of light from two luminous points to the retina. The rays from the point *a* on passing through the cornea, lens, &c., are collected on the retina at *b*. Those from *a'* meet at *b'*, and thus the lower point becomes the upper.

hypermetropic eye, parallel rays of light are brought to a focus at a point beyond the retina, so that divergent or parallel rays cause diffusion circles and a blurred image. This may be corrected by means of convex glasses which make the rays convergent before they strike the corneal surface, and thus enable them to be sooner brought to a focus by the dioptric media of the eye.

Presbyopia is the name given to a change in the perfectness of accommodation frequently accompanying old age. The lens probably becomes less elastic and the ciliary muscle weaker, so that the change in form required to see near objects is difficult or impossible to attain. Biconvex lenses help to overcome the difficulty.

Defects of Dioptric Apparatus.

In common with all dioptric instruments the eye has certain optical defects which tend to interfere with the distinctness of the image.

Chromatic aberration is due to the breaking up of white light into

several colours, owing to the different coloured rays of which ordinary light is composed, possessing different degrees of refrangibility. We see this in the spectrum and in the coloured rings of the marginal part of a biconvex lens made of a single kind of glass. This form of aberration can be corrected by making lenses of two kinds of glass, one of which counteracts the dispersion caused by the other. Optical instruments may thus be made achromatic. This defect is minimised by the iris, which cuts off the marginal rays in which it is most apt to occur. Possibly the different density of the various parts of the dioptric media may have a correcting effect on the chromatism of the eye. Further correction takes place in the nerve-centres which receive the sensation, for just as we mentally re-invert the image, we are unconscious of the colour. At any rate, the chromatic aberration is so slight that it needs certain artifices to make it observable.

Spherical aberration depends upon the fact that luminous rays, on passing through a convex lens, strike the various parts of its surface at different angles, and hence are differently refracted. The rays striking the margin of the lens are more bent than those passing through the centre, and hence the former come sooner to a focus. Thus a luminous point gives rise to a diffused figure, which is circular in perfectly centered dioptric systems, but is stellate in our eyes where the centering of the lenses is not absolutely accurate. Spherical aberration causes us no inconvenience, as the iris only allows the more central rays to pass, in which its influence is not noticed.

Another optical defect in our eyes is *astigmatism*, depending upon some irregularity of the curvature of the cornea, which may be bent more horizontally than vertically, or *vice versâ*. In either of these cases the light in the vertical and horizontal planes will be differently refracted, so that lines drawn in the two directions will require different adjustments to see them distinctly. This may be recognized if we gaze with one eye at a centre from which many sharply-defined lines radiate: some of the lines cannot be seen distinctly, unless we move the eye or change its accommodation. When the greater curvature extends evenly over the whole diameter of the cornea it gives rise to what is called *regular astigmatism*, and when the unevenness is localized to one part of the cornea surface it is called *irregular astigmatism*.

The astigmatism which may be called physiological is not noticed by the individual, but pathological astigmatism often occurs and requiries cylindrical glasses to correct it.

Entoptic images are those which depend on the presence of some opacity or difference in density in the transparent media of the eye

itself. They look like variously-shaped specks moving over the field of vision. They are only remarkable when we look at an evenly coloured object or through a pin-hole in a black card. In using the microscope they often annoy the unpractised observer.

The Iris.

Functions.—It has already been mentioned that the motions of the iris alter the size of the *pupillary aperture* through which the rays of light must pass, and while it *regulates* the amount of light admitted, it also acts like the *diaphragm* of an optical instrument, and always

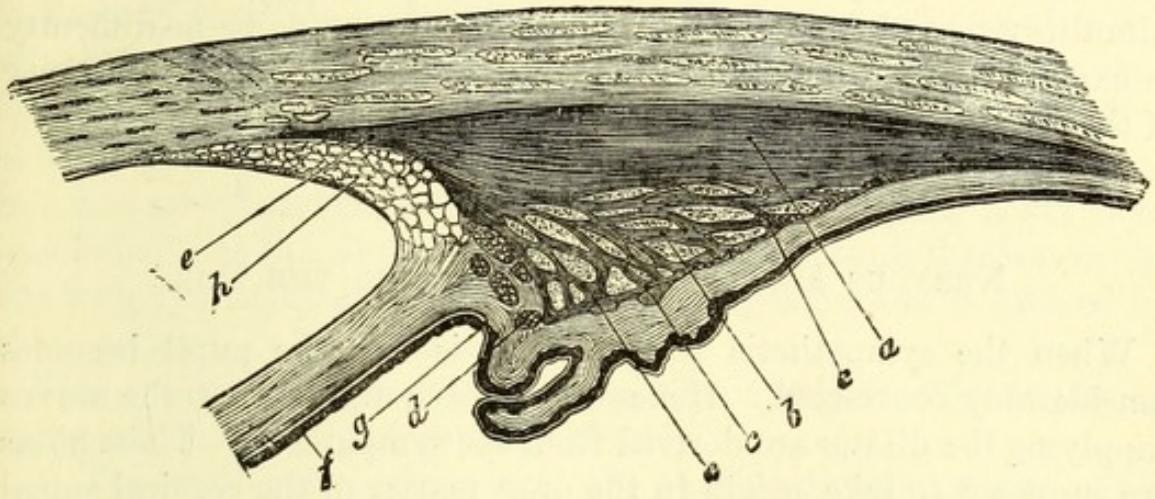


Fig. 227.—Section through the ciliary region, showing the relation of the iris (*f*) to the choroid (*g*) and the ciliary muscle (*a*), which arises from the margin of the cornea at (*e*), and passes towards the choroid to the right, where it separates the latter from the sclerotic. Some bundles of circular fibres are shown, one marked (*d*).

cuts off a large amount of the marginal rays. The great importance of not allowing the rays which would traverse the margin of the lens to enter the eyeball can be understood after what has been said of spherical and chromatic aberration. The iris also contracts when the eye is *adjusted for near vision*, independent of the amount of light by which the object is illuminated. This action is of advantage, because the more convex the lens becomes in viewing near objects, the greater is the aberration of the marginal rays. If the iris did not contract in near vision, the closer an object was brought to the eye, the greater would be the tendency to indistinctness caused by spherical aberration.

In *structure*, the iris consists of a framework of delicate connective tissue, like that of the choroid coat, containing many blood-vessels. On its posterior surface is a dense layer of pigment cells called the uvea, which gives the eye its colour. The act of contracting the

pupil is performed by a very definite set of *instriated muscular fibres* forming the sphincter which surrounds the margin of the pupil. The sphincter muscle seems always to be more or less in action, because if it be paralysed, the pupil dilates. The muscular character of the dilator mechanism has been doubted from the fact that radiating muscular fibres have not been satisfactorily demonstrated under the microscope. Certainly the sphincter is the most distinctly contractile, for strong electric stimulation always causes contraction of the pupil, and shortly after death the pupils dilate from the relaxation of the sphincter. If we admit the active dilatation of the pupil, we must assume that the power of the sphincter dies more quickly than that of the dilator, or that it at once relaxes when it has lost the stimulus reflected from the retina. There appears to be no difficulty in explaining the dilatation of the pupil as the effect of the elasticity of the tissue and the changes in vasomotor influences.

Nervous Mechanisms Controlling the Iris.

When the sympathetic in the neck is cut, the pupil becomes considerably contracted. Hence it has been argued that the nerves supplying the dilator are derived from the sympathetic. These fibres are supposed to take origin in the grey matter of the cervical spinal cord. The sympathetic also supplies the walls of the vessels, and thus controls the amount of blood going to the iris, and this contraction of the pupil has been explained as due to vascular engorgement. It is argued that though the vasomotor mechanisms may co-operate in dilatation, they cannot be its only cause, as the widening of the pupil may occur in a bloodless eye. Since the other tissues are elastic, and antagonize the sphincter, paralysis of that muscle would give rise to dilatation even in anæmic mydriasis.

The *constricting nerve mechanism* of the sphincter muscle is distinct, and more definitely understood. Its common action is reflex : the stimulus starts in the retina, and travels along the optic nerve as an afferent channel to the corpora quadrigemina, where there is a centre governing the contractions of both irides. The efferent impulses are sent by the third nerve to the lenticular ganglion, and thence by the short ciliary nerves to the eyeball.

In accommodation for near objects three muscles act together, their movements being "associated" by the central nerve mechanisms. The same voluntary effort that causes the *ciliary muscle* to contract, makes the *sphincter* of the iris contract, and also causes the

internal rectus to move the eye inwards. The voluntary nerve centre must be in intimate relation with the reflex centre, which keeps up the tonic action of the sphincter iridis.

We have then *central* governors for the ciliary and iris movements. The ciliary muscle and sphincter of the pupil are both caused to act by the will, and the sphincter alone is excited by means of a centre, which reflects the stimulus arriving from the retina by the optic nerve to the branches of the third nerve. The dilator of the pupil, if a muscle, is also kept in gentle tonic action by the impulses sent from the spinal cord with the vaso-motor impulses, *viâ* the sympathetic; but some think that the blood supply and tissue elasticity explain the dilatation.

Further, from the undoubted facts (1) that some reflex contraction of the pupil may be produced by stimulating the retina, even when the eye is cut off from the brain centres, and (2) that the local effect of atropia in dilating, and calabar bean in narrowing the pupil, seem in a measure independent of the central nerve organs, it has been concluded that there must also be some local nerve mechanism in the eye which is capable of reflecting nerve impulses, and is affected by these poisons.

The student must carefully bear in mind all the circumstances under which the pupils contract, namely :—

1. The application of strong light to either retina, causes reflex stimulation of the ciliary nerves of both eyes.
2. Stimulation of the nasal or ophthalmic branches of the fifth afferent nerve reflexly excites the sphincter.
3. Contraction of the pupil is "associated" with accommodation for near objects.
4. Similar "associated" contraction always accompanies inward movement of the eyeball.
5. During sleep, or as the result of vasomotor disturbances in the brain (anæmia), the pupil contracts.
6. Under the influence of physostigmin, nicotin, and morphia.
7. From any stimulation of the optic or third nerves or the corpora quadrigemina.

The circumstances in which the pupils are found to be dilated are equally important from a practical point of view, namely :—

1. In the dark or with insensitive retinæ.
2. Irritation of the cervical sympathetic.
3. Under the influence of atropin, daturin, &c.
4. In asphyxia or dyspnœa from venosity of the blood.
5. Painful sensations from the skin, &c.

The Ophthalmoscope.

When we look into the eye the pupil appears quite black, no matter in what position we place the light. The reason of this is that the retina can only be made visible by the light reflected outwards from it, and that the portion of the rays which is reflected by the retina is so refracted in passing out of the eye, that it occupies

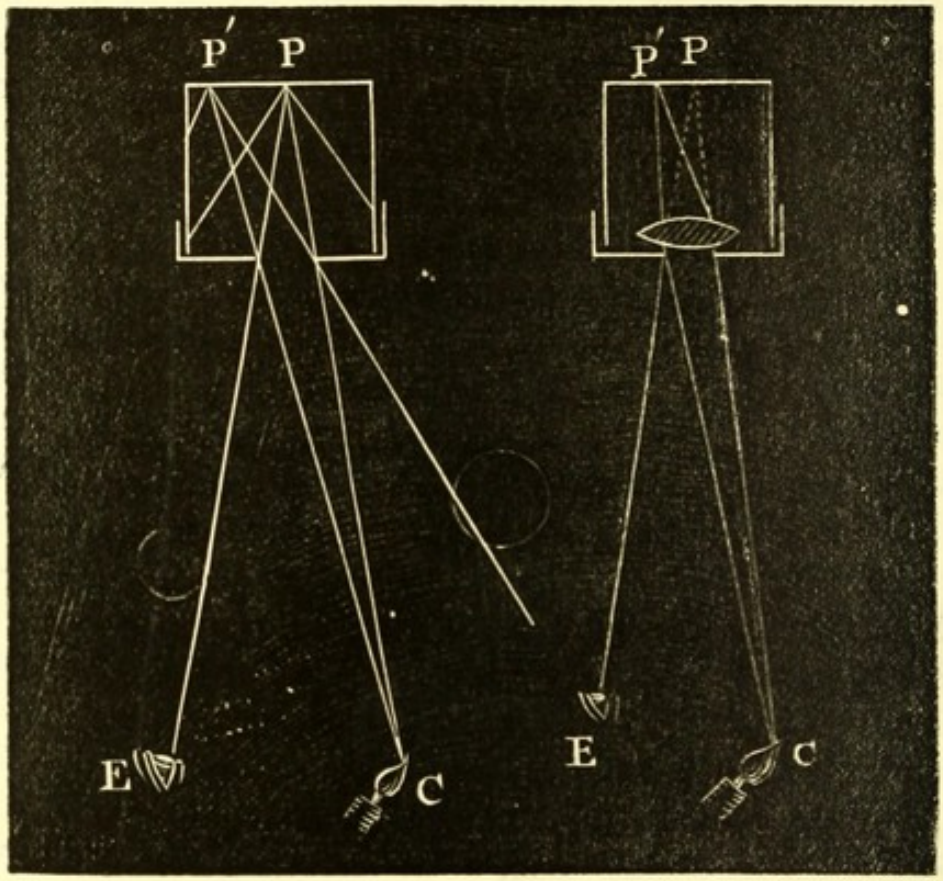


Fig. 228.—Diagram showing the effect of a lens on the rays of light reflected from the paper (retina) in the experiment given in the text. E. Observer's eye. C. Point of illumination. On the left the reflected rays diverge, and some pass to E. On the right they are refracted by the lens to form a cone.*

exactly the same path as that travelled by the light on its way from the point of illumination to the eye. Consequently, unless the eye of the observer be placed directly in this path, none of these reflected rays can reach it to enable him to see the fundus.

That is to say, the lens and other refractive media that bend the rays of the ingoing cone of light to a focus on the retina also bend those of the outgoing cone reflected from the retina to a focus at the point of illumination.

* "How to Use the Ophthalmoscope," by Edgar A. Brown, p. 32.

The fact that the blackness of the interior of the eye is caused by the lens, &c., can be shown by a simple experiment.

Blacken the inside of a pill-box (about an inch deep), paste printed paper on the bottom, and cut a round hole half an inch in diameter in the lid. By illuminating the interior of the box obliquely the print can be easily recognised. If a convex lens of one inch focus be placed behind the opening, the paper cannot even be seen, and the opening looks black like the pupil with any position of the light. The paths traversed by the rays in this experiment may be seen in Fig. 228.

In the left-hand figure of the above woodcut the first case is illustrated. Here the divergent rays passing from the candle C to the surface P P′ are reflected in various directions from it; those which strike the blackened interior of the box are absorbed; others emerge through the hole in the lid, and reaching the eye placed at E, enable the print at P to be seen.

The second case is shown in the right-hand figure. Here, instead of diverging till they reach the bottom of the box, the rays are refracted by the lens to a focus at the point P′, from which they pass back through the lens, and are thereby bent to a cone converging to the source of light. No rays pass in the direction E, so the interior of the box looks quite black.

In attempting, then, to view the fundus, the observer must either place his head in the line of light, or the light in the line between the observed eye and his own; in short, his eye must lie in the line of reflection, in order to see the fundus. If we could see through the source of light, the above object would be accomplished. Helmholtz, by reflecting light into the eye by means of transparent glass plates, originally succeeded in seeing through the plates some of the rays reflected from the fundus. In this method, however, the power which enables the glass plates to reflect the luminous rays towards the eye, also robs the observer of much of the light sent back from the retina by reflecting it towards the source of light, and the remaining rays which penetrate the glass cannot give a clear image of the retina.

A simple instrument, the *ophthalmoscope*, is now in general use for examining the retina. This consists of a concave mirror of short focal distance, which is substituted for the transparent reflecting plates. The rays converging from the mirror to the eye are brought to a focus on the retina, and thence some are reflected outwards, and converged by the dioptric media to the hole in the centre of the mirror, behind which the observer's eye is placed to receive the cone of converging rays.

If the observer place his eye and the mirror at a distance of about 3 cm. from the observed eye, and the refraction of both eyes be normal, he can see an enlarged virtual image of the fundus. If the refraction of either eye be abnormal, it must be corrected by a suitable lens placed behind the aperture in the mirror. This is called the *direct method* of examination.

To overcome the inconvenience and difficulty of this mode of examination the *indirect method* is usually employed. In it a convex lens of 20 or 40 diopters is used in addition, enabling the observation

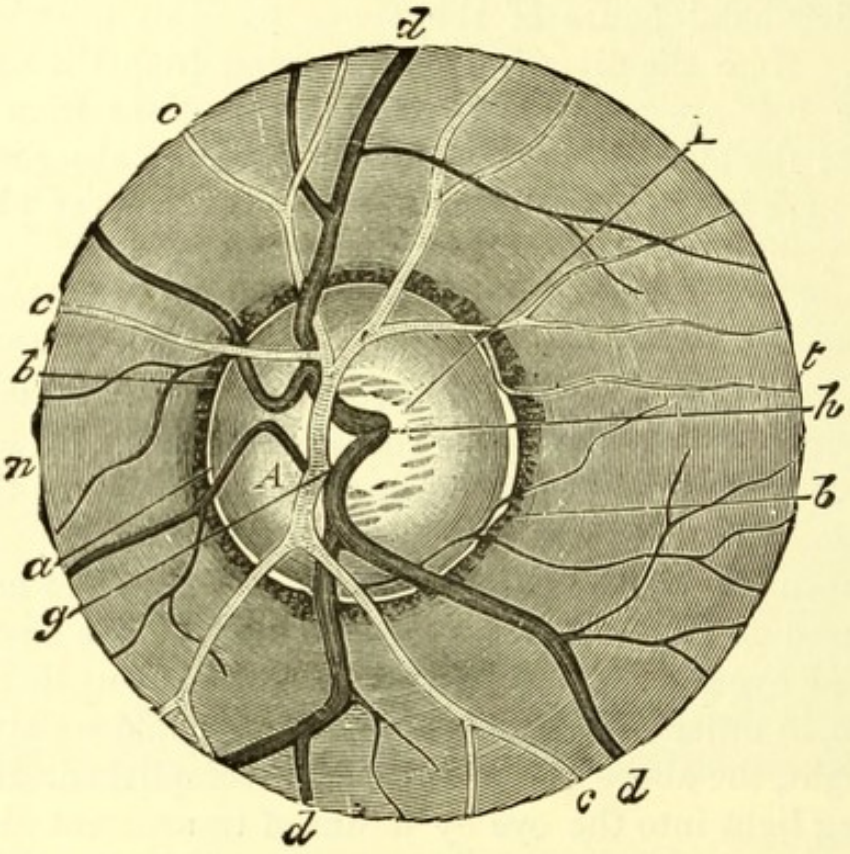


Fig. 229.—Ophthalmoscopic view of fundus of eye, in which the central artery (*g* and *c*) and the corresponding veins (*h* and *d*) are seen coursing through the retina from the optic disc (*A*).

to be made at a more convenient distance. When the eye has been illuminated, the lens is placed at its proper focal distance (2 or 1 inches respectively) in front of the eye. By the converging power of the lens a real inverted image of the fundus is formed in the air a couple of inches to the observer's side of the lens, and can be seen by him through the aperture in the mirror, if he hold his head at a distance to suit his refraction.

With this instrument a round whitish part is seen a little to the nasal side of the axis of the eye, where the nerve pierces the dark choroid coat. This is called the optic disc. The fundus now, when

lighted up, does not look black, but is of a lurid red colour, owing to the great vascularity of the choroid coat. Over this red field are seen a number of blood-vessels, which start from the centre of the optic disc, and radiating over the fundus send branches to the most anterior parts that can be seen. These are the branches of the vessel which runs in the centre of the nerve. In the very axis of the eye a peculiar depression, free from branches of the blood-vessels, can be seen. This central depression (fovea centralis) differs a little in colour from the neighbouring parts during life, and turns yellow at death, and hence has been called the "yellow spot." The retina is so transparent that we cannot see it with the ophthalmoscope, but the radiating vessels (central arteries and veins of the retina) lie in it and belong to the nervous structure only.

The ophthalmoscope has proved of inestimable value not only to the ophthalmologist, but also to the physician, as a means of arriving at an accurate knowledge of disease. Hence it has become more a pathological than a physiological instrument.

Light Impressions.

The retina is that part of the eye by which the physical motions called *light* are changed into what are known physiologically as nerve-impulses, by means of which the impression of light is excited in the brain. In reaching the retina the light is not altered from the light with which physicists experiment, but at the retina this physical motion is stopped. The optic nerves no more convey the light waves from the eye to the brain than the tactile nerves carry the objects that stimulate their endings. They only send a nerve-impulse which the retina, on its exposure to the light, excites in the terminals of the optic nerve. Any form of stimulation, if applied to the optic nerve, will cause an impulse to pass to the brain, which there sets up the sensation of light. Thus we are told by persons who have had their optic nerves cut that the section was accompanied by the sensation of a flash of light but not pain. Any violent injury of the eye-ball causes a flash of light to be experienced. This fact has long since been recognised in a practical manner, for a blow implicating the eye-ball is vulgarly said to "make one see stars." Also, without violent injury, if we close the eyes and turn them to the one side and then press through the lid with the point of a pencil on the other side of the eyeball, we have a sensation of a point or ring of light from the retinal stimulation. Thus we say that the

specific energy of the optic nerves excites a sensation of light, and the adequate stimulus of the nerve terminals of the organ of vision is light. The first question that arises is, what part of the retina does this important work of stimulating the optic nerve when light impinges on its terminals?

The Function of the Retina.

The retina is a complex peripheral nervous mechanism composed of many elements, the special functions of which are not adequately known. It spreads over the fundus of the eye, but where the nerve pierces the coats of the eyeball there is nothing but nerve fibres, and hence no retina, properly so called, exists at the *optic disc.*

The structure of the retina varies in different parts, but the following layers can be recognised in most regions (Fig. 230). The exceptions will be mentioned afterwards.

Lying next to the hyaloid membrane is the layer of *nerve fibres* which radiate from the optic disc to the ora serrata near the ciliary region. The fibres spread evenly over the fundus except at the central point (fovea centralis), which they avoid by passing above and below it. These fibres form the inner layer of the retina.

Next to the fibres is a layer of *nerve cells,* which seem to have one pole connected with a fibre from the optic nerve, while from the other side two or three poles send processes into the adjacent layers of the retina. The cells are numerous near the yellow spot.

Outside the foregoing are four less distinctive layers. The first is broad and *granular;* next, two layers of peculiar *nuclear* bodies are found, with a thin dense one of granular material between them.

Outside these, and separated by a fine limiting membrane, is the terminal layer of the retina. It consists of *rods and cones* which are connected with those parts of the retina already named, and are embedded in the protoplasm of pigmented epithelial cells, which, on their outer face, show a striking hexagonal outline (Fig. 233). The rods and cones are easily torn away in histological sections from the pigmented epithelium, but the epithelium and rods and cones are so intimately connected in their development and function that they ought to be regarded as a single layer.

A retinal nerve fibril may be said to have the following course: entering the eyeball from the optic nerve at the *porus opticus,* it reaches the immediate vicinity of the hyaloid membrane, and runs a certain distance in contact with that membrane, it then turns outwards towards the choroid and enters a nerve cell. From the nerve

cell pass a couple of filaments which traverse the various granular and nuclear layers—where they probably inosculate with the filaments from other cells—and finally terminate in a rod or a cone.

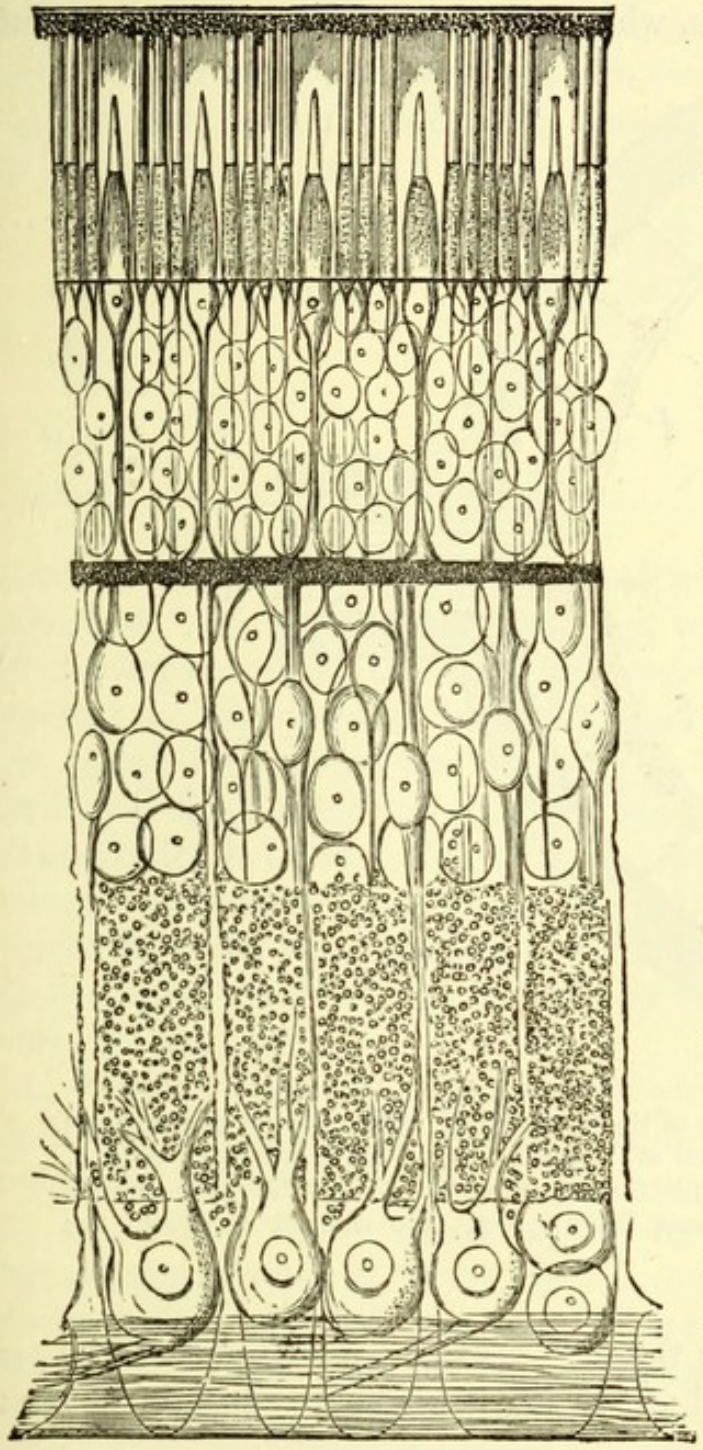


Fig. 230.—Diagrammatic section of retina showing the relation of the different layers in the posterior part of the fundus (not the *macula lutea*). (Schultze.)

The rods and cones are the ultimate terminals of the nerves, and they lie in the active protoplasm of the peculiar, pigmented epithelial cells.

This outer layer, consisting of rods and cones lodged in epithelial

protoplasm, is the effective part of the retina. Of this we have the following evidence :—

1. The *anatomical fact* that the rods and cones must be regarded as the nerve terminals of the optic nerve.

2. That the macula latea, where the retina is chiefly made up of

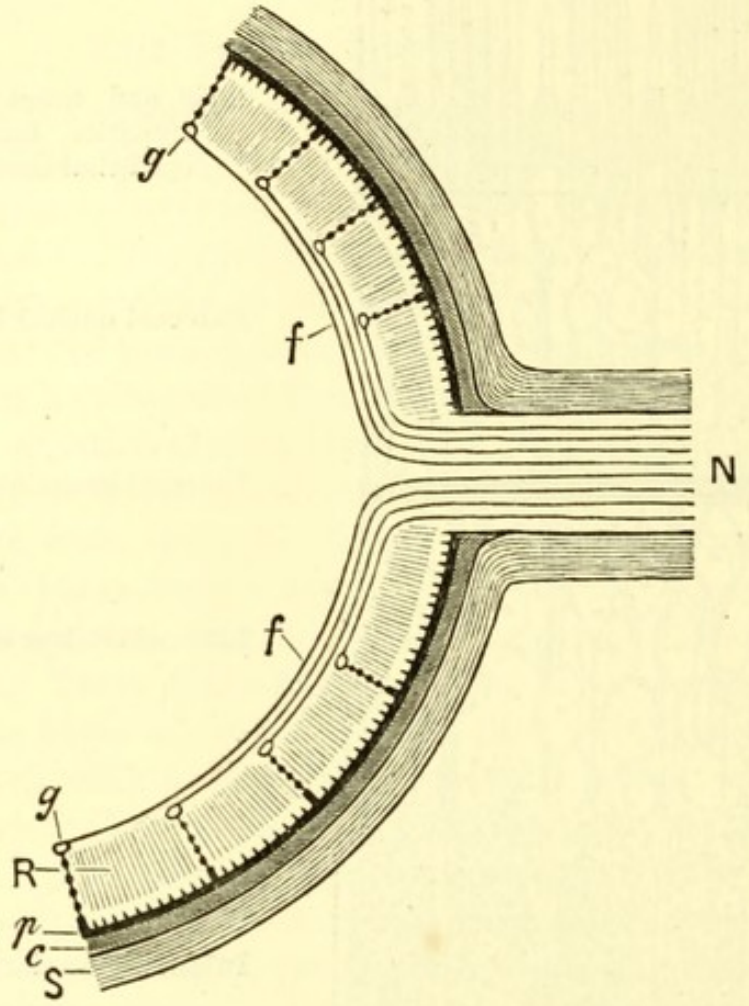
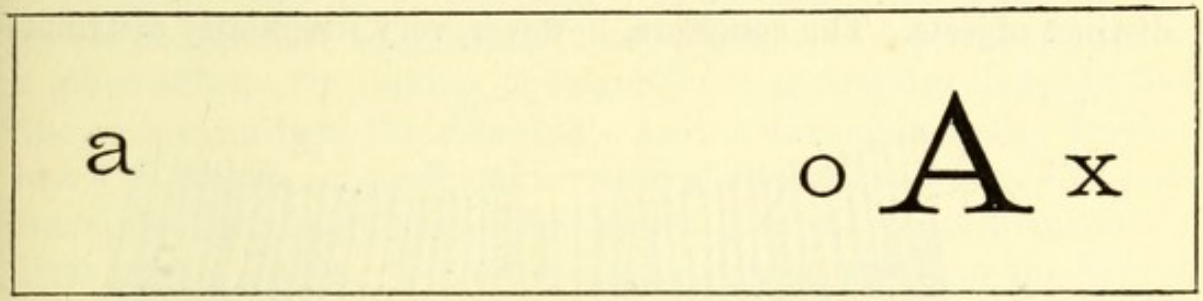


Fig. 231.—Showing the course of the fibres of the optic nerve N, as they pass along the inner surface of retina R, to meet the ganglion cells *g*, whence special communications pass outwards to the layer of rods and cones in the pigment layer *p*, next the choroid *c*, within the sclerotic *s*.

the cone layer, is very much the most sensitive part, and near the ora serrata, where the rods and cones are less developed, sight is least acute.

3. *The blind spot.*—From the facts that where the optic nerve enters the eyeball there are no rods and cones, and though the nerve fibres are fully exposed to the light, they cannot appreciate it, this part, the optic disc, is called the "blind spot." This shows that the nerve fibres are quite insensitive to light, and that we must look to the terminals for its appreciation. The existence of the blind spot can

be demonstrated as follows. Shut the left eye, and hold the left thumb, at ordinary reading distance, in front of the other eye. While the right eye is fixed on the left thumb, bring the right thumb to within about four inches, and move it slowly an inch or so, from side to side. A little practice soon enables one to find a place when the right thumb nail disappears. It also can be demonstrated by keeping the right eye, the left being closed, *fixed on the small letter* "**a**" and moving the page to or from the eye very slowly; a distance



(about 10 inches) may thus be reached when the large letter "**A**" is quite lost. On approaching the page when "**A**" is invisible, the letter reappears from the inner side and "**x**" is first seen; on withdrawing the page it comes into view from the outer side, and "**o**" is first seen. By varying the direction and noting the near and far limits of "**A**'s" being invisible, one can mark out the extent of the fundus which is blind. This blind spot is not noticed in ordinary vision, as we have habitually overcome the deficiency by the experience derived from the use of both eyes since infancy. By rapid movements one eye hides the deficiency, as is found when attempting the experiment just described.

4. *Purkinje's figures.*—The fact that when the eye is illuminated in a peculiar way we can see the shadow of the blood-vessels which lie in the inner layers of the retina thrown upon the outer layer of rods and cones, also shows the latter to be the sensitive part. This phenomenon, known as "Purkinje's figures," can be demonstrated as follows. Close the left eye in a dark room, with an evenly dull-coloured wall, and while you stare fixedly at the wall with the right eye turned inwards hold a candle to its outer side so that the light can reach the fundus of the eye from the side. With a little practice the least motion of the candle will bring out an arborescent figure on the wall, which exactly corresponds to the retinal vessels. It may also be seen by arranging a microscope so as to show a bright light, on looking into the instrument and either moving it or the head slightly but constantly, the shadows of the retinal vessels will be clearly seen as though they were under the instrument.

Retinal Stimulation.

Point of greatest sensitiveness.—As in the perception of two points of contact with the skin, so we find the retina ceases to be able to distinguish the difference between two luminous points, if they be brought to a focus at a distance of less than ·002 mm. from one another. This distance nearly corresponds to the diameter of the cones, and it is supposed that the rays from two luminous points must come upon two different cones in order to be visible as two distinct objects. The cones are, however, very irregularly distributed

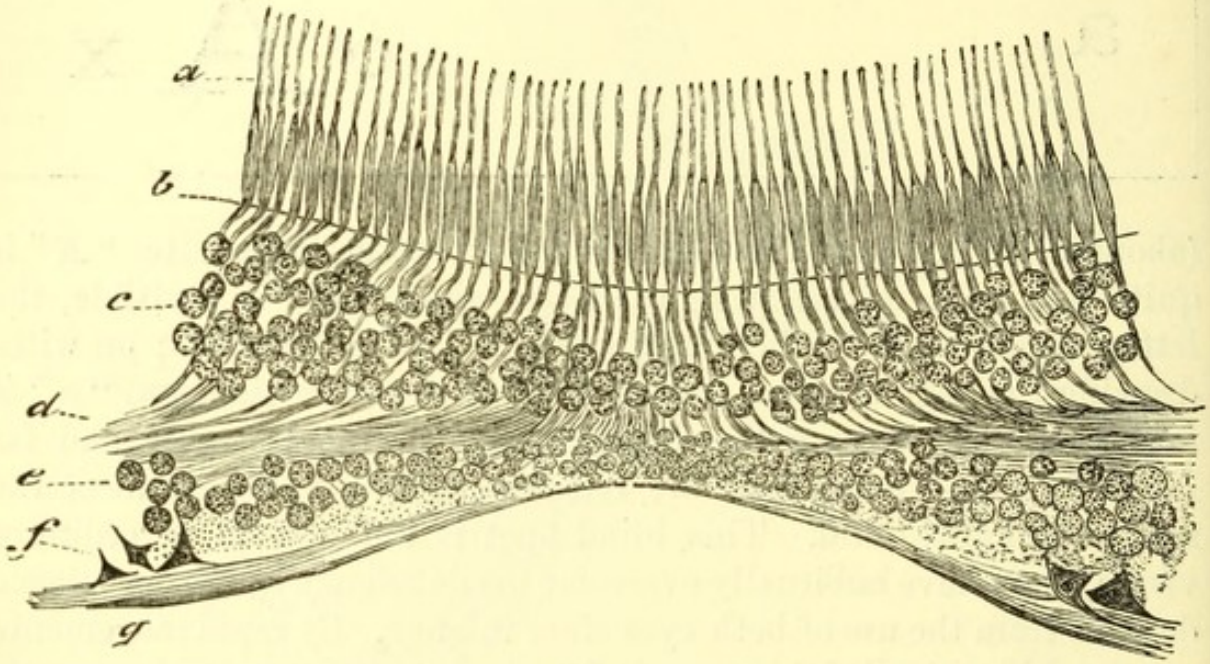


Fig. 232.—Section of the retina at the yellow spot, showing the great number of cones (*a*) at this point, and the thinness of the other layers. (Cadiat.)

over the retina, being packed closely together at the yellow spot, and scattered more and more widely apart as one passes to the peripheral parts of the retina. It is only at the yellow spot that the cones, which are here very thin, are so close together as ·002 mm., so that this estimation of the size of visual areas could only hold good of the yellow spot, and towards the peripheral parts the power of discrimination must be much less keen. This is found to be the case, for in ordinary vision everything seen clearly with a sharp outline must be brought upon the yellow spot. This is spoken of as "direct vision." The images falling on the other parts of the retina are but dim and indistinct outlines, and these are spoken of as "indirect vision."

Variations in stimulation.—The stimulus need only be applied for a very short time to cause a distinct sensation, for we can readily see

a single electric spark; and it need only affect an extremely small part of the retina, as a minute speck of light can be seen by direct vision, and a very feeble ray suffices to stimulate the retina. The amount of stimulation produced depends upon (1) the intensity of the light, *i.e.*, the amount of light received in a given area; (2) the duration of its application; (3) the extent of retina to which it is applied; (4) the part of the retina stimulated; (5) the darker the background the weaker the illumination we can distinguish, *i.e.*, the greater the stimulating effect of a weak light; (6) by fatigue the retina loses its power of appreciating light, and more stimulus is required to produce a given effect. On waking, the daylight is at first dazzling, but soon the retina can bear the stimulus. An increase of intensity does not cause an exactly proportional increase of stimulation, for we find the more the light is intensified the less we notice a fresh increment of light until a degree of intensity is arrived at, when no further addition can be detected, and the light becomes blinding. The less the absolute intensity of two lights the better we distinguish any difference that may exist between them.

Duration.—The effect lasts for an appreciable time after the stimulus has been removed, particularly if the light be very intense. This can be observed when a brilliant point is in rapid motion; instead of a point a streak of light is seen. Thus part at least of the trail of falling stars is caused by the persistence of the stimulation, and a luminous body rapidly rotated gives the impression of a circle of fire.

When the stimulus is very intense, such as an electric light, or when we look at a bright object like the globe of a lamp steadily for some time, the effect persists, and after the eyes are shut we see a faint image of the object. This is called the *positive after image.* If the retina be exposed to a bright light until it be fatigued, and then suddenly turning we gaze at a white wall, the bright part of the positive after image is replaced by a dark figure which is termed the *negative after image.*

A strong stimulus applied to the retina spreads from the part upon which the bright image falls to those in its immediate neighbourhood, so that the bright object looks larger. This phenomenon is called *irradiation.* It helps to explain many of the peculiarities of vision.

Excitation of Nerve Impulse.

The question now arises, how do the retinæ, or rather their outer layers, convert light into a nerve stimulus? It would appear quite

out of the question that the 394 to 760 billions of waves of light per second could mechanically excite the nerve terminals as the waves of sound are believed to excite the endings of the auditory nerve. We know that light has a very distinct action on many chemical combinations, such as reducing salts of silver and gold, &c. We, therefore, imagine that the light waves may set up, in the outer layer of the retina, certain intermolecular motions or *chemical changes*, the result of which is that the nerve fibres are stimulated to activity and transmit an impulse to the brain. The light possibly produces a change in the outer layer of the retina which in some respects may be compared to that which occurs on a sensitive photographic plate. In some respects only, because, while the chemical change on the sensitive plate persists so as to give rise to a permanent photograph, in the eye it only lasts for the brief moment during which we can recognize the positive after image. The chemical change in muscle may be compared to the explosion of gunpowder, in giving rise to force, but not in the result produced in the materials. For in muscle the chemical change causing the contraction is rapidly repaired, while in the powder permanent alteration of the substance is produced. In the retina a new sensitive plate is at once produced by the restoration of the normal condition of the molecules, and similarly its explosive qualities are at once restored to the muscle.

The view that the layer of rods and cones undergoes a chemical change on exposure to light which suffices to excite the optic nerve, receives support from the observation that a colour of a red or purplish hue exists in the outer part of the rods and that this colour changes when exposed to the light. But this so-called *visual purple* has not an inseparable connection with vision, since it is absent where the retina is most sensitive, *i.e.*, the fovea centralis, where there are no rods, and further, frogs with blanched eyes, seem to see quite well. Certain rays of light have a distinct *thermic influence*, and hence the possibility exists that the nerve impulse is started in the retina by some delicate thermic stimulus.

Against the chemical and thermic origin of the retinal stimulation may be urged the fact that the rays of the spectrum which are most efficient in exciting chemical and thermic variations (ultra-violet and ultra-red respectively) do not excite any nerve impulse in the retina.

The *pigmented epithelial cells* of the retina have been observed to change their shape slightly, and definitely to alter the position of the pigment granules they contain when exposed to light. When we remember how sensitive to light the protoplasm of many unicellular infusoria is, we cannot be surprised that the protoplasm of the retinal

epithelium is affected by it. In the pigment cells of the frog's skin we are familiar with a change in shape and in the arrangement of their pigment granules in response to different light stimuli. We know further that in the nervous centres nerve impulses often originate in protoplasm under the influence of slight changes in temperature or nutrition. It would hardly be too much to assume, then, that the retinal epithelium has some important share in the transformation of light into a nerve stimulus. The arguments pointing to the rods and cones as the essential part of the retina apply equally well to the pigmented epithelium, for they are so dove-

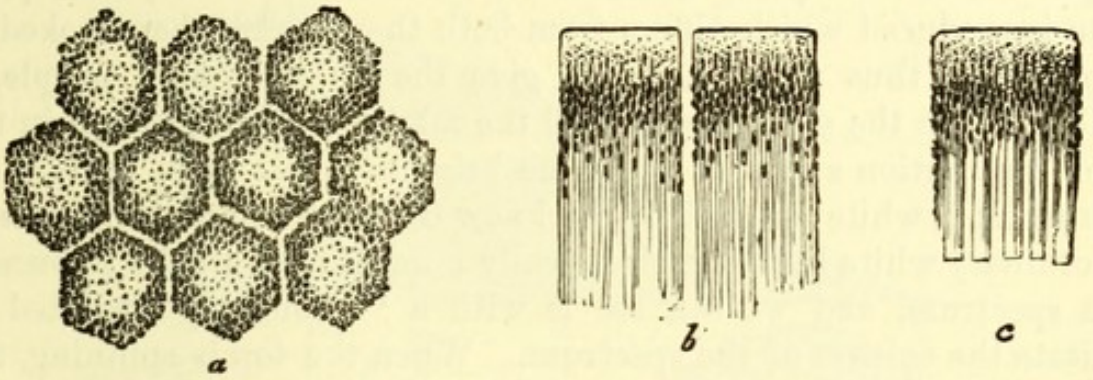


Fig. 233.—Epithelial cells of the retina. *a*, Seen from the outer surface; *b*, Seen from the side as in a section of the retina; *c*, shows some rods projecting into the pigmented protoplasm.

tailed one into the other that practically they form but one layer. They are not known to be connected with the nerve fibres, but they may still be influenced by the light, and communicate the effect to the contiguous nerve terminals, which appear to be elaborately adapted to the appreciation of subtle forms of stimulation.

Colour Perceptions.

If a beam of white sun-light be allowed to pass through an angular piece of glass it is decomposed into a number of colours which may be seen by looking through the prism, or may be thrown on a screen, like that of a camera. These colours, which look like a thin slice of a rain-bow, are together called the *spectrum*. The white solar light is thus shown to be a compound of rays of several colours which possess different degrees of refrangibility and hence are separated on their way through the prism. The violet rays are the most bent, and the red the least, so that these form the two extremes of the visible spectrum. The difference of colour depends upon the different lengths of the waves, the vibrations of violet (762 billions

per sec.) being much more rapid than those of red (394 billions per sec.) Beyond the visible spectrum at the red end there are other rays which though they look black to the eye, are capable of transmitting heat. This thermic power is best developed in these ultra-red rays and fades gradually towards the middle of the spectrum. Outside the violet are ultra-violet rays, which, though non-exciting to the retina, are very active in inducing many chemical changes. Only those ether vibrations which have a medium length, can stimulate the retina.

If two different colours be mixed before reaching the retina, or be applied to it in very rapid succession one after the other, an impression is produced which differs from both the colours when looked at separately; thus violet and red give the impression of purple, a colour not in the spectrum. If all the colours of the spectrum in the same proportion and with the same brightness fall upon the retina, the result is white light. This we know from the common experience of ordinary white light, which is really a mixture of all the colours of the spectrum, and we can see it with a "colour top" painted to imitate the colours of the spectrum. When the top is spinning, the colours meet the eye in such rapid succession that the stimulus of each falls on the retina before that of the others has faded away, and thus many colours are practically applied to the retina at the same time, and the top looks nearly white.

It has been found that certain pairs of colours taken from the spectrum when mixed in a certain proportion produce white. These are *complementary* to one another. The complementary colours are :—

Red and peacock-blue.	Yellow and indigo.
Orange and deep blue.	Greenish-yellow and violet.

If colours which lie nearer to each other in the spectrum than these complementary colours be mixed, the result is some colour which is to be found in the spectrum between the two mixed.

The perception of the vast variety of shades of colour that we can distinguish, can only be explained by means of this colour-mixing. We may suppose (with Hering) that there are three varieties of material in the retina, each of which gives rise to antagonistic or complementary colour sensations according as they undergo increased or decreased molecular activity. These antagonistic states being produced by the complementary colours. Thus one substance gives the sensation of black or white, another red or green, another yellow or blue, according as they are in exalted or diminished activity. A

varying degree of these stimulations can be easily shown to give many differences of shade.

Or we may assume that there are three primary colours which overlap one another in the spectrum so as to produce all the various tints. These are *red*, *green*, and *violet;* the arrangement of which may be diagrammatically explained (Fig. 234).

We must in this case further assume (Young, Helmholtz) that there are in the retina three special sets of nerve terminals, each of which can only be stimulated by red, green, or violet respectively, and the innumerable shades of colour we see, depend upon mixtures of

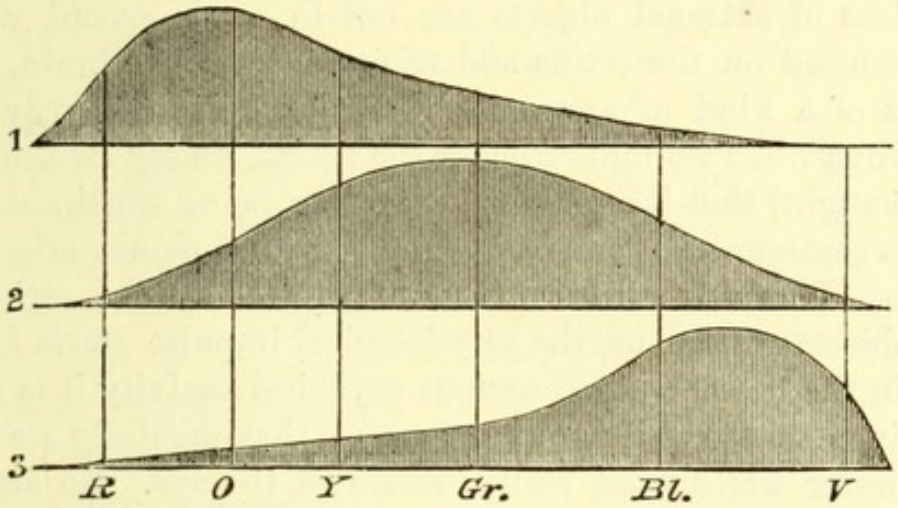


Fig. 234.—Diagram of the three Primary Sensations: 1 = red; 2 = green; 3 = violet.
The letters below are the initials of the colours of the spectrum.
The height of the shaded part gives extent to which the several primary sensations are excited by different kinds of light in the spectrum.

different strengths of these primary colours, producing different degrees of stimulation of each set of nerve terminals.

The view that such special nerve apparatus exists for red, green, and violet is supported by the fact that the most anterior or marginal part of the retina is incapable of being stimulated by red objects, which look black when only seen by this part of the retina. This inability to see red may extend over the whole retina, as is found in some persons who may be said to be "red-blind." If we investigate our negative after images, after looking for a long time at a red object, we find them to be greenish blue. That is to say, the nervous mechanism for receiving red impressions is fatigued, and that of its complementary colour is easily stimulated.

Mental Operations in Vision.

Our visual sensations enable us to perceive the existence, position, and correct form of the various objects around us. For visual perception much more is necessary than the mere perfection of the dioptric media of the eye, and of the retinal nerve-mechanisms. Besides the changes produced in the retina by light and the excitations in the nerve cells of the visual centre, there must be psychical action in other cells of the cortex of the brain. This psychical action of the brain consists of a series of conclusions drawn from the experiences gained by our visual and other sensations.

Our ideas of external objects are not in exact accord with the image produced on the retina and transmitted to the brain, but are the result of a kind of argument carried on unconsciously in our minds. Thus when no light reaches the retina, we say (without what we call thought) that it is dark; our retina being unstimulated, no impulse is communicated, and the sensation of blackness arises in our sensorium. When luminous rays are reflected to the retina from various objects around us, the physiological impulse starts from the eye, but in the brain, by unconscious psychical activity it is referred in our minds to the objects around us, so that mentally we project into the outer world what really occurs in the eye. So also, from habit, we re-invert in our minds the image which is thrown on the retina upside-down, by the lens, and so unconscious are we of the psychical act that we find it hard to believe that our eyes really receive the image of every thing inverted, and our minds have to reinstate it to the upright position.

One of the most important means employed to enable us to form accurate visual perceptions is the varied motion which the eyeballs are capable of performing.

Movements of the Eyeballs.

The eyeballs may be regarded as spherical bodies, lying in loosely fitted sockets of connective tissue padded with fat, in which they can move or revolve freely in all directions, in a limited degree. The muscles which act directly on the eyeball are six in number. Four *recti* passing from the back of the orbit are attached to the eyeball, one at each side and one above and below, not far from the cornea. These move the front of the eye to the right or left, up or down respectively. Two *oblique* passing nearly horizontally outwards, and a little backwards, are attached to the upper and under

surface of the eyeball respectively. These muscles can slightly rotate the eye on its antero-posterior axis, the upper one drawing the upper part of the eyeball inwards, and its antagonist the lower, drawing the lower part inwards, so as to rotate the eyeball in an opposite direction round the same axis.

The internal and external recti draw the centre of the cornea to or from the median line respectively, directly opposing one another.

As the direction of the superior and inferior recti is different from that of the axis of the eyeball, they draw the outer edge of the cornea, not its centre, up and down respectively, and at the same time tend to give the eyeball a slight rotation in the same direction as the corresponding oblique muscles. The tendency to rotation is counteracted by the antagonistic oblique muscle when simple elevation or depression is performed.

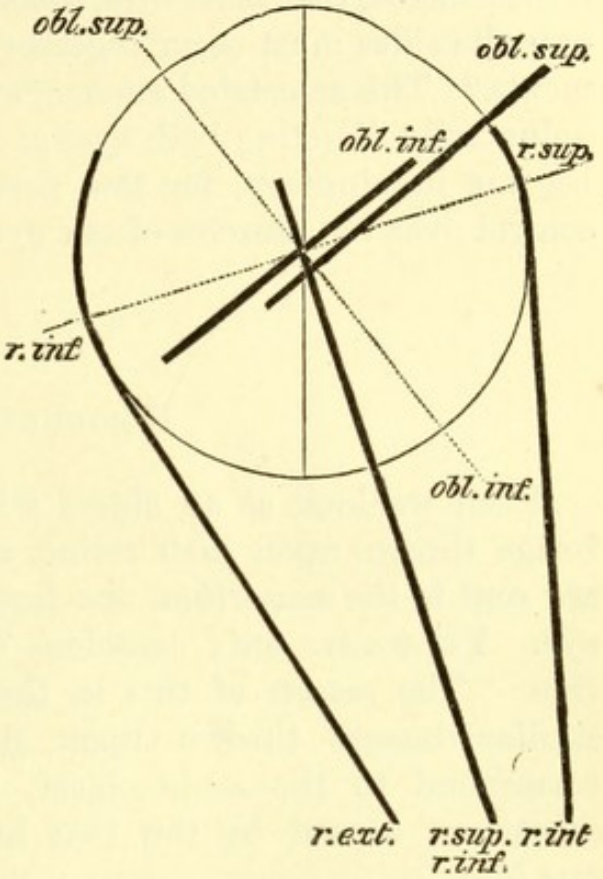


Fig. 235.—Diagram of the direction of action of the muscles of the eyeball, which is shown by the dark lines. The axes of the rotation caused by the oblique and upper and lower recti are shown by the dotted lines. The inner and outer recti rotate the ball on its vertical axis, which is cut across. The abbreviated names of the muscles are affixed to the lines.

Thus pure abduction or adduction only requires the unaided action of the internal or external recti, while direct depression of the eye requires the combined action of the inferior rectus and superior oblique, and direct elevation requires the superior rectus and inferior oblique to act together. The oblique movements are accomplished by various combined co-ordinations of movement of the different muscles.

From the foregoing it is obvious that the simplest movements of the eye require the co-operation of different muscles.

The diagram shows the directions towards which the different muscles tend to draw the eyeball.

In the ordinary movements of both eyes more than this is necessary.

Both eyes must move in the same direction at the same time, now to the right, now to the left, so that while the external rectus moves the right eye to the right side, the internal rectus moves the other eye in the same direction. The co-ordination of the movements of the eyeball is so arranged, that the contractions of the external and internal recti of opposite sides must occur together, and are called "associated movements." This associated movement has been acquired by the habit of voluntarily directing both eyes at the same object, and has gradually become involuntary, for few persons have the power of exerting control over the muscles of one eye alone.

Binocular Vision.

When we look at an object with both eyes we have a separate image thrown upon each retina, and therefore two sets of impulses are sent to the sensorium, one from the right and one from the left eye. Yet we are only conscious of the occurrence of one stimulation. The reason of this is, that experience has taught us that similar images thrown upon certain parts of the two retinæ correspond to the same object, and in our minds we fuse the sensations caused by the two images so that they produce but one idea.

These points of the retina which are thus habitually stimulated by the same objects are called "corresponding points."

Besides being of great use in making up for such deficiencies as the blind spots (which are not corresponding points) binocular vision is useful for the following purposes :—

To judge of *distance*. When using one eye only, some knowledge of distance may be gathered by the force employed to accommodate, but a much more accurate judgment can be formed when both eyes are used and the muscular sense of the ocular muscles, employed in converging the eye-balls for near objects, gives further evidence of their distance.

In judging of *size*, in the same way, with one eye, we can only have an idea of the apparent size of an object, which will vary with its distance. With a knowledge of apparent size and distance such as is gained by binocular vision, we can come to a fairly accurate conclusion as to the size of an object.

To judge of the relative distances of objects so as to see *depth* in the picture before our eyes, binocular vision is necessary. If one eye

alone is used we see a flat picture without having an accurate idea of the relative distances of the different objects. With each eye, however, we get a slightly different view of each object, and thus we are helped to a conclusion as to their exact distances and shapes, and arrive at fairly correct judgments as to their form, &c.

CHAPTER XXXIII.

HEARING.

Just as impulses travelling along the optic nerves can only give rise, in the sensorium, to impressions of light, so impulses passing to the sensorium *viâ* the auditory part of the *portio mollis* of the seventh pair of cranial nerves can only excite impressions of sound, and any stimulation of that nerve gives rise to sound sensations.

The peripheral end of the special nerve of hearing is distributed to an organ of very peculiar construction situated in the internal ear, which, from its complexity, has been called the *labyrinth*. The nerve-endings are spread out between layers of fluid, so that they must be stimulated by very gentle forms of movement; and when we consider their delicacy, we cannot be surprised that even sound vibrations suffice to stimulate these terminals and transmit nerve impulses to the brain. The organs of hearing of mammalia are so deeply placed in the petrous part of the temporal bone, that special mechanisms have to be adopted to convey the sound with sufficient intensity from the air to the fine nerve-terminals. These make up a complex piece of anatomy which will be briefly referred to presently.

Sound.

Before attempting to describe the complex mechanisms by which sound is conveyed from the air to the nerve-endings, some notion must be formed of what sound is from a merely physical standpoint. By means of the sense of hearing we form an idea of sound, and here the knowledge of sound ends with many people, since they only think of it as something they can hear. A physicist, however, regards sound in a different way. He knows that it is produced by the vibrations of elastic bodies, such as a tense string, a metal rod, or an elastic membrane. These vibrations, being communicated to the air, are conveyed by it to our nerve-endings, where they set up a

nerve impulse. The impulse is transmitted along the nerve to the brain, and there gives rise to the sensation with which we are familiar as sound.

The vibrations of the air are wave-like movements depending upon a series of changes of density in the gases, the particles of which move towards or from one another, and transmit the motion to their neighbours, so as to propagate the sound wave. To demonstrate these vibrations a special apparatus must be used.

When a tuning-fork is struck it is thrown into vibration, and a sound is given forth. But the vibrations are often so rapid and so small, that the motion of the tuning-fork cannot be appreciated by the eye. But if a fine point be attached to one prong of the tuning-fork—or, indeed, any elastic body, such as a bar of metal—and this point be brought into contact with a moving smoked surface, such as has been already described for similar records, a little wavy line is drawn, showing that the vibrating fork moves up and down at an even and regular rate. Each up and down stroke indicates a vibration. The length of the wave, as drawn on the evenly-moving surface of the recorder, shows the amount of time occupied by each vibration. This is always found to be the same for a tuning-fork of a given pitch, and thus the recording fork is in constant use by the physiologist as an exact measure of small intervals of time. The *pitch* of the note depends upon the *rate* or *period* of vibration, a tone of a certain pitch being simply a sound caused by so many vibrations per second. The quicker the vibration the higher the note, and the slower the deeper, until at the rate of about thirty per second, no sound is audible. Whether a note be produced by a metal fork, a tense string, or any other vibrating body, if the number of vibrations per second be the same, the note must have the same pitch.

The elevation of each vibration as seen in the tracing made by a recording fork is different at different times. When the fork is first struck, the waves are high and well marked; the excursions of the recording prong become less and less extensive as the fork gradually ceases to vibrate, and the sound diminishes; or in other words, as the sound produced becomes fainter, the vibrations become smaller. The amount of excursion made by the vibrating body is spoken of as the *amplitude* of the vibration, and upon it depends the *loudness* or intensity of the sound. The pitch of a tone bears no relation to the amplitude of the waves of vibration, but depends upon their rate; while its loudness is quite independent of the period occupied by the vibrations, but is in proportion to the square of the amplitude of the waves.

So far only *tones* or musical notes have been mentioned. They are produced by vibrations occurring at perfectly regular periods. The simpler and more regular the vibrations, the purer the tone. The great majority of the sounds we are accustomed to hear are not pure tones, but are the result of an association of vibrations bearing some relation to one another. When the variety of vibrations is very great, their intervals irregular and out of proportion, they give rise to a discordant sound called a noise. So long as such commensurability exists in the rate of the vibrations as to produce a sound not disagreeable to the sense of hearing, it may be called a note.

By the use of a series of different resonators, each of which is capable of magnifying a certain tone, it can be shown that the clearest and purest notes of our musical instruments are far from being simple tones, but are really compounds of one prominent note or fundamental tone, modified by the addition of numerous *over-tones* or *harmonics*. If one blows forcibly across an orifice leading to a space in which a small amount of air is confined, such as the barrel of a key or the mouth of a short-necked flask or bottle, either a clear shrill or dull booming sound is heard, which varies in pitch according to the proportions of the air-containing cavity. This dull note is a simple tone. It is devoid of character, and in this respect differs greatly from the notes produced by a musical instrument. The notes of every instrument have certain characters or *qualities* which enable even an unpractised ear to distinguish them.

This *quality*, which is independent of the pitch (*i.e.*, rate of vibration), or the intensity (*i.e.*, amplitude of wave), is called the *colour* or *timbre* of the note. It depends on the number, variety, and relative intensity of the over-tones or harmonics, which accompany the notes. So that really the *timbre* or quality of a note, and therefore the special characters of the different musical instruments, is produced by their impurity, or the complexity of the over-tones which aid in producing them.

All elastic bodies can vibrate, and therefore are capable of conducting sounds. Sound vibrations can be transmitted from one body to another placed in contact with it. From a hard material the waves are readily communicated to the air, and this is the ordinary medium by means of which sound is transmitted to our organs of hearing. In the old experiment of placing a small bell under the glass of an air-pump, and making the tongue strike after the air has been removed, the fact that no sound is produced shows that the medium of the air is essential for the transmission of sound-vibrations.

The transmission of waves of sound from the air to more dense materials, such as those which surround our auditory nerve-terminals, takes place with much greater difficulty than that from a solid to the air, and we find a variety of contrivances by which the gentle air-waves, arriving at the ear, are collected and intensified on their way to the labyrinth.

The medium of the air is not necessary in order that sound may reach the internal ear. Nor is the route through the outer canal, and the drum and its membrane, the only one by which the vibrations can arrive at the cochlea. The solid bone which surrounds the labyrinth is in direct communication with all the bones of the head, and sound can travel along these bones, and reach the nerve-endings. This can easily be proved by placing the handle of a vibrating tuning-fork against the forehead, or better still, against the incisor teeth. The sound, although previously hardly audible, at once becomes quite distinct, or even appears loud.

This direct conduction through the bones of the head is, under normal conditions, of little use to man ; but attempts have been made, in cases where the ordinary auditory passages were rendered inefficient by disease, to gather the vibrations on an elastic plate, and apply this to the teeth. This direct conduction of sound is very valuable in determining the seat of disease in cases of deafness. So long as a clear sensation of sound reaches the brain through the bones of the head, we know that the important nerve-endings and their central connections are unimpaired, and conclude that the disease lies in the mechanical conducting parts of the hearing organ.

In fishes, where the labyrinth is the only existing part of the auditory apparatus, it is embedded in the cranium, and the sound waves arriving through the medium of water, are directly conveyed to the nerve-endings by the bones of the head. An air-containing tympanum would rather impede the hearing of these animals.

The parts of the ear through which sound passes before it reaches the nerve, are separated into three departments, viz. :—(1) the auditory canal and external ear ; (2) the middle ear, tympanum or drum, which is shut off from the latter by the tympanic membrane ; and (3) the labyrinth.

Conduction of Sound-vibrations through the External Ear.

External ear.—In man, the muscles are so poorly developed that he can hardly move the external ear or pinna perceptibly, and the

part commonly called the ear is of little use. We know this, because the outer ear may be quite removed without materially affecting the power of hearing. The sound reflected from the pinna may be excluded, without reducing the intensity of that heard, by placing a little tube in the auditory canal. Birds hear well without any outer ear. But the moveable ears of many animals are, no doubt, useful in helping them to ascertain the direction of a sound by catching more of the vibrations coming towards their pinna. That the external ear may be of some use, even to man, one is led to believe, by the natural readiness with which a person with dull hearing supplements it by means of his hand. In this act the ear is pushed away from the head to an angle of about forty-five degrees, and its projection is considerably increased.

External auditory meatus.—The auditory canal is a crooked and irregular passage, getting rather wider as it approaches the tympanic cavity. It is the seat of some short, stiff hairs, which help to prevent the entrance of foreign matters. It is supplied with a peculiar modification of sweat glands, which secrete a waxy material that helps to keep the walls of the canal and the outside of the membrane moist and soft.

The elastic column of air in any circumscribed space resounds more readily to some one tone, varying according to the capacity of the space ; thus resonators of different pitch are formed. Different tubes have different notes when blown into, so the auditory canal has a note of its own, and if the canal be short, the note is one of a very high pitch. When a tone of the same pitch as that to which the canal is tuned strikes the ear, it is unpleasantly magnified, and such sounds are called shrill and disagreeable. Upon the more ordinary sound-vibrations, however, the auditory canal has little or no effect.

Conduction of Sound-vibrations through the Tympanum.

The end of the auditory canal is closed by the *membrana tympani*, which slopes obliquely from above downwards and inwards, in which direction its size is greater than if it were straight across the canal. This membrane is not flat, for the central point is drawn in by the handle of the *malleus*, which is firmly attached to it. The membrane is thus held in the shape of a very blunt cone, somewhat like a Japanese umbrella, the apex of which points inwards towards the cavity of the drum. The peculiar form of the membrane of the drum is of great importance for distinct hearing.

As every confined volume of air has a certain *proper tone* to which it resonates readily, so a membrane of a given size and tension has a proper tone (*self-tone*), the vibration period of which it follows naturally. This tone varies with the tension, as may be seen in a common drum, the note of which can be changed with the tension

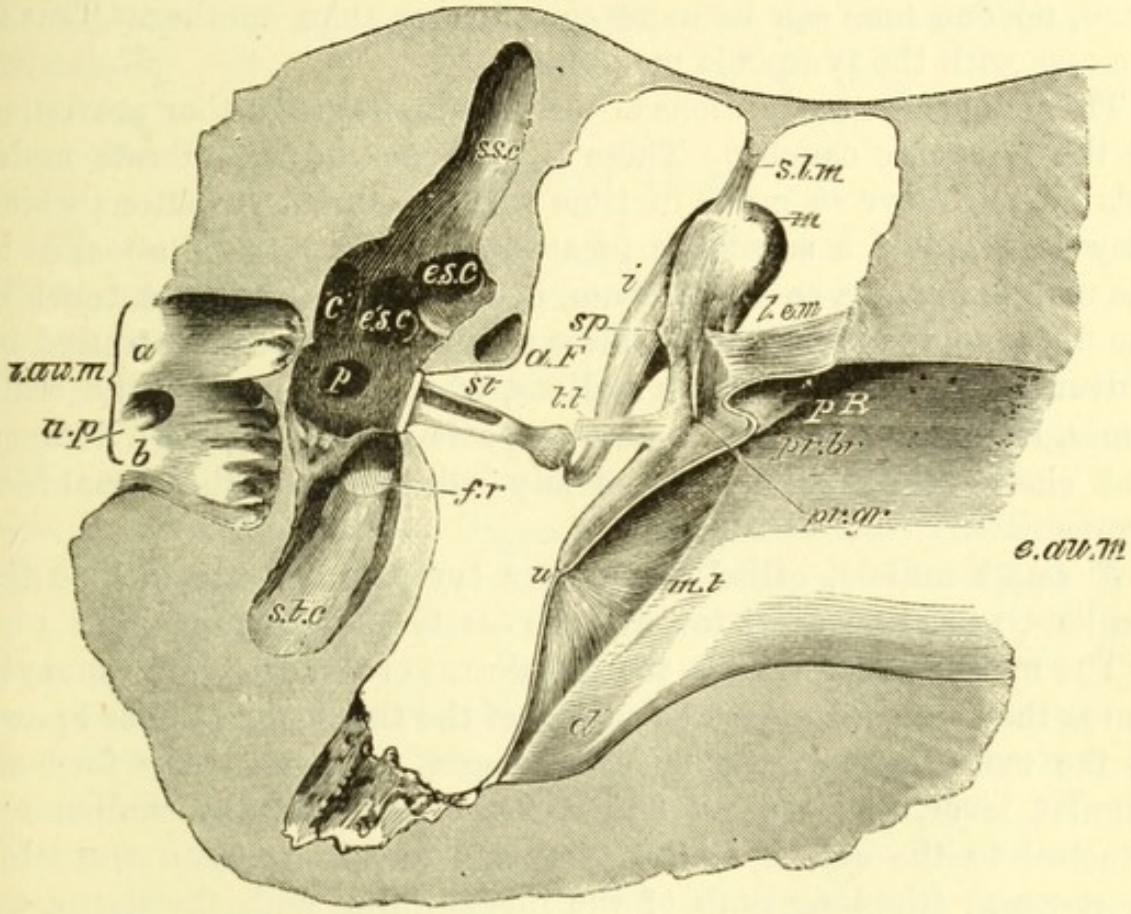


Fig. 236.—Diagram of the tympanum, showing the relation of the ossicles to the tympanic membrane and the internal ear. The tympanum is cut through nearly transversely, and the cavity viewed from the front (left ear). (Schäfer.)

Membrane, *m.t*, of the drum to which the handle of the malleus, *m*, is attached at *u*. Head of malleus, *m*, which is held in position by its suspensory ligament *s.l.m.*, and external ligament *l.e.m*; long process of incus, *i.*, connecting malleus and stapes *s.t.*, the base of which closes the oval opening of the vestibule *p*. External auditory meatus *e.au.m*. Internal auditory meatus *i.au.m*, where the two parts of the auditory nerve enter, *a* and *b*.

of its parchment; the tenser the membrane, the higher the pitch. If the membrane of the drum of our ears were set to one tone, our hearing would be imperfect and unpleasant, for we should be wearied by the reiteration and persistence of the one note. This does not occur; the tympanic membrane has no marked self-tone, and no succession of vibrations follows the first effect of the sound waves.

Any self-tone is prevented by the conical shape of the membrane, which is partly due to the traction of the handle of the malleus.

If a stretched membrane, such as that of a drum, be drawn out at its centre, so that it is no longer a flat surface, its tension is different at the centre and the periphery, being greatest at that point at which it is drawn, and gradually decreasing towards the margin. Since the existence of a tone of a definite pitch depends upon a certain degree of tension, if no two parts of the membrane are similarly tense, no one tone can be more conspicuous than another. This is the case with the tympanic membrane.

The independent vibrations of the membrane are further prevented by the tympanic ossicles. These little bones do not vibrate molecularly, but move *en masse* in time with the sound-vibrations which they deaden. If a substance incapable of vibrating be attached to the membrane of a common drum, it ceases to vibrate. A touch of the finger to the membrane suffices to check the sound produced by a drum. The handle of the malleus, which is joined to the other bones, being fixed to the membrane, acts in this way as a damper, and checks the continuance of any vibration in the membrana tympani.

A small muscle, called the tensor tympani, is attached to the malleus, so as to draw it towards the cavity of the tympanum.

The motions occurring in the membrane of the drum are conveyed across the tympanic cavity by means of the three small bones known as the *malleus*, the *incus*, and the *stapes*. These ossicles form an angular lever, one arm of which (the handle of the malleus) is attached to the centre of the tympanic membrane, and the other shorter arm (the long limb of the incus) unites with the stapes, the base of which is held by the secondary tympanic membrane in the oval opening leading into the vestibule. The stapes is attached at right angles to the extremity of the inner arm of the lever, being jointed to the long arm of the incus. This little angular lever works round an axis which passes from before backwards through the head of the malleus, and lies above the membrane of the drum, the two points which act as the bearings or pivots of the motion being the slender process of the malleus in front, and the short limb of the incus behind.

When the tympanic membrane vibrates in response to the sound waves of the air, it moves, and the handle of the malleus moves in and out with it. The body of the incus, being fixed by a firm joint to the head of the malleus, must follow these movements, and cause the oval base of the stapes to press in or draw out the membrane which separates the tympanum from the vestibule. Thus the vibrations of the air communicated to the tympanic mem-

brane are conveyed across the tympanic cavity to the liquid in the labyrinth.

A small muscle—the stapedius—is attached to the stapes near its junction with the incus, and pulls upon it in such a direction that the bone is drawn out of the direct line of motion. This action, possibly, reduces the more ample vibrations of the tympanic membrane, which might injure the delicate mechanism of the labyrinth.

Eustachian Tube.

The tympanum is connected with the pharynx by means of the Eustachian tube which, though habitually closed, is opened for a moment by swallowing and other motions of the pharynx. On these occasions air can pass in or out of the tympanum, so that the pressure on both sides of the membrane of the drum is equalised. When there is too much or too little air in the tympanic cavity, the tympanic movements are impeded. This difficulty is felt during a cold in the head, when the tube is occluded, and the oxygen being absorbed, the pressure in the tympanic cavity is reduced. Or in performing what is known as Valsalva's experiment, *i.e.*, holding the nose and blowing air into it, whereby the Eustachian tubes are opened, and too much air is often retained in the tympanum, so that the pressure from within is higher than that from without, and hearing becomes dull. If the act of swallowing be then performed, the feeling of tension leaves the ears as the excess of air escapes, and hearing becomes as acute as before.

The Eustachian tube also acts as a way of escape for any fluid that may be secreted by the epithelial lining of the tympanic cavity. The amount of fluid is so small, that the occasional opening of the tube suffices, under ordinary circumstances, for its complete escape. When increased by disease, it may collect in the tympanum, and require catheterisation.

If the tubes were permanently open, we should suffer from two great disadvantages. At every breath, during ordinary respiration, some change in tension of the air contained in the cavity of the drum would occur and impair hearing; the vibrations of the air in the pharynx, produced by the voice, would enter the drum directly, and give rise to an exaggerated shouting noise.

Conduction through the Labyrinth.

Every motion of the oval base of the stapes causes a wave to pass along the liquid in the labyrinth. The bony case of the internal ear being firm, the wave travels through all parts of the internal ear. Through the *cochlea* it arrives at the *inner tympanic membrane* which closes the *fenestra rotunda*, and separates the cavity of the tympanum from the scala tympani of the cochlea. The waves have a very complex route in passing from the *fenestra ovalis* closed by the stapes to the membrane closing the cochlea. By means of the liquid lying around the membranous labyrinth—*perilymph*—the waves pass up the *vestibular spiral* of the cochlea, and arriving at its summit, they descend by the *tympanic spiral* to the fenestra rotunda. In this course they pass over and under the fluid—*endolymph*—contained in the membranous canal of the cochlea in which the special nerve terminations are placed.

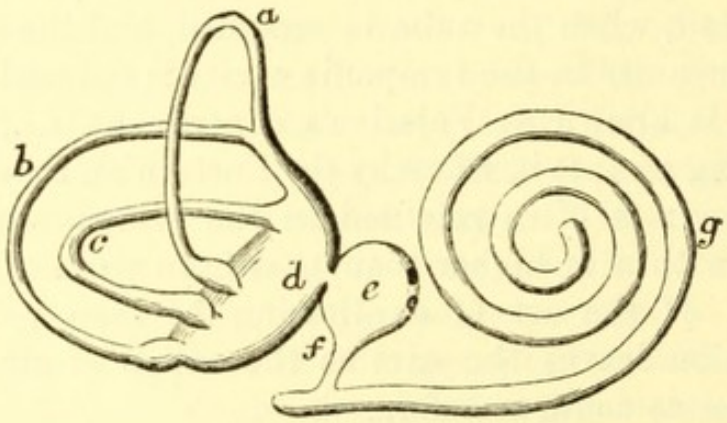


Fig. 237.—Diagram of the membranous labyrinth, all of which is filled with endolymph and surrounded by perilymph. *a*, *b*, *c*, semicircular canals opening into the ventricle *d*; *e*, the saccule from which the uniting canal, *f*, leads into the membranous canal of the cochlea, *g*. (Cleland.)

For the construction of the labyrinth the student is referred to the text-books of anatomy, as space only admits of a brief account of the special arrangements of the nerve-ending.

Terminals of the Auditory Nerve.

The nervous mechanisms which are most important for the appreciation of tones are those situated in the cochlea.

The nerve-endings found in the membranous sacs in the vestibule are connected with peculiar epitheloid cells, to which are attached

fine bristle-like processes. These processes lie in the *endolymph*, and are related to calcareous masses called *otoliths*. Waves in this endolymph possibly bring the otoliths into collision with the hairs, and thus give a stimulus to the nerve-endings. Noises may be heard from this, but no impressions of tone can be appreciated. The use of the nerves going to the other parts of the labyrinth—*ampullæ* of the *semicircular canals*—is doubtful, and probably not immediately connected with hearing.* The coils of the cochlea are throughout their entire length partially divided by a bony shelf projecting from the central axis into the spiral cavity. This is called the *osseous spiral lamina*. In the fresh state the separation of the spiral canal into an upper (vestibular) and a lower (tympanic) coil is completed by a membranous partition, which stretches from the bony spiral lamina to the opposite side of the spiral canal. This is called the *membranous spiral lamina*, and forms the base upon which the special nerve-endings of the organ of hearing are placed. An extremely delicate membrane called the *membrane of Reissner* stretches from the upper side of the spiral partition obliquely upwards to the outer wall of the spiral cavity, so as to form a canal and cover the special organ, shutting off a portion of the vestibular coil which lies over the membranous spiral lamina. The *canal of the cochlea* thus formed is triangular in section. Its floor is made up chiefly of the membranous spiral lamina, particularly the part called the *basilar membrane*, while the oblique roof is composed of only the thin membrane of Reissner. The canal follows the turns of the cochlea, lying between the vestibular coil and that leading to the tympanum, and is filled with a fluid (endolymph) which is quite separate and distinct from that in the vestibular or tympanic coils (perilymph).

The cochlear division of the auditory nerve passes into little tunnels in the central bony column around which the coils of the cochlea turn, and gives off a series of spiral branches which run through the osseous spiral lamina to reach the membranous portion. A collection of ganglion cells connected with the radiating nerve-fibres is found lying in the spiral canal of the osseous lamina. Passing through the bony spiral the nerves reach the basilar membrane, which, as before mentioned, forms a great part of the membranous spiral lamina, and upon which the organ of Corti is placed.

The *organ of Corti*, placed upon the basilar membrane within the membranous canal of the cochlea, is made up of a series of peculiarly

* Compare equilibration, in connection with which they will be described.

curved bars or fibres, called the *rods of Corti*, and some epitheloid cells provided with short, bristle-like processes. The rods of Corti

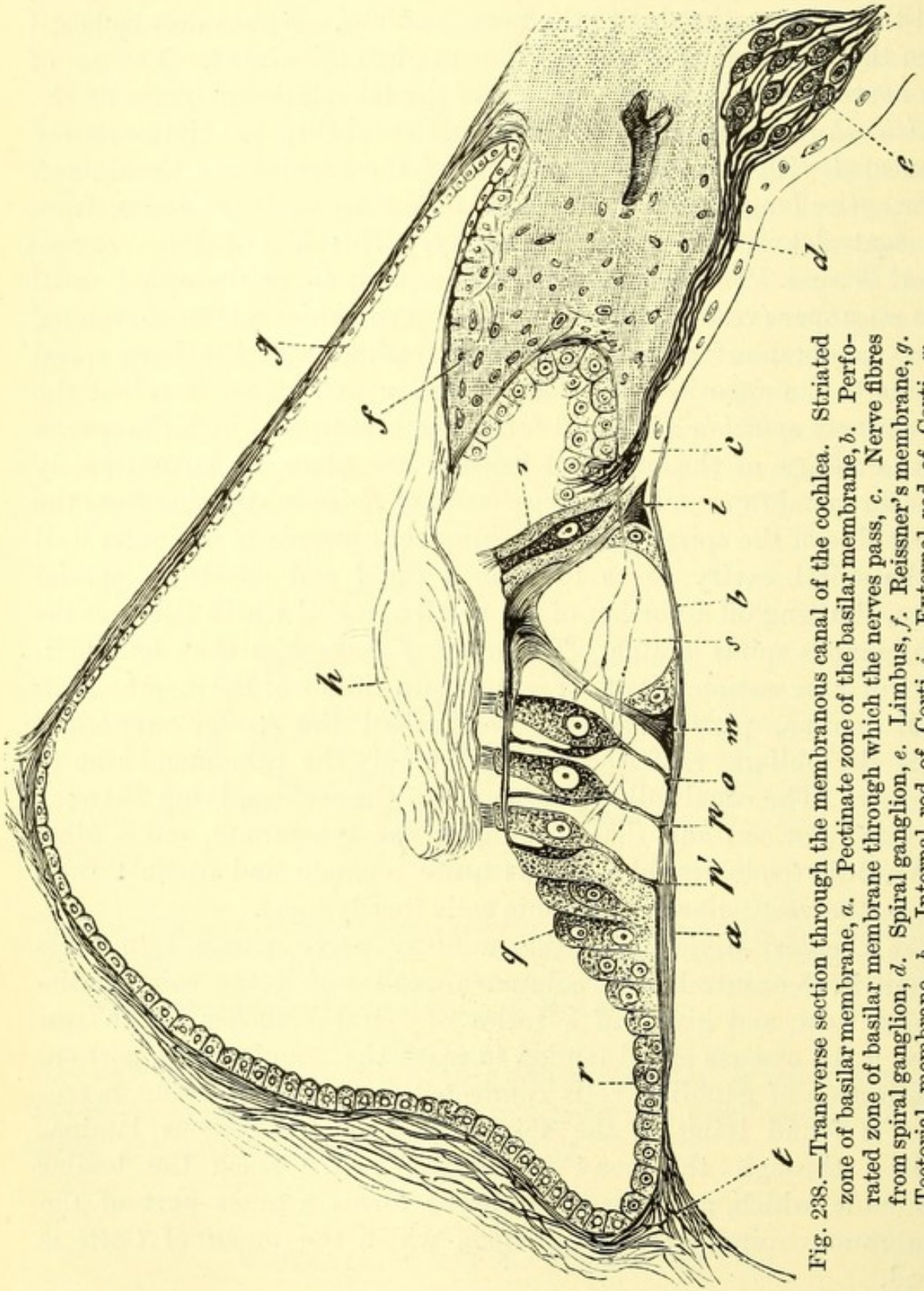


Fig. 238.—Transverse section through the membranous canal of the cochlea. Striated zone of basilar membrane, *a*. Pectinate zone of the basilar membrane, *b*. Perforated zone of basilar membrane through which the nerves pass, *c*. Nerve fibres from spiral ganglion, *d*. Spiral ganglion, *e*. Limbus, *f*. Reissner's membrane, *g*. Tectorial membrane, *h*. Internal rod of Corti, *i*. External rod of Corti, *m*. Special cells receiving nerve terminals, *o*, *p*, *p'*. Epithelial cells covering the basilar membrane, *q*. Nerve fibres, *s*. Spiral ligament, *t*. (Cadiat.)

are fixed by their broad bases upon the basilar membrane, and unite above in such a way that the outer and inner rods form a bow or arch. The spiral series of rods thus propped up against each

other leave a small space or tunnel under them, which runs the entire length of the basilar membrane. Beside these rods of Corti are placed rows of cells of an epithelial type into which the nerve-endings pass. From the upper surface of these cells, on a level with the apex or junction of the rods, a number of hair-like processes project. A delicate *reticulated membrane* lies over the rods and the cells, and seems to be lightly attached to their surface, while the hairs pass through its meshes.

The *basilar membrane* is made up of fibrous bands held together by a delicate membrane. The fibres pass transversely across the spiral canal of the cochlea, so as to subtend the bases of the outer and inner rods. The basilar membrane gradually becomes wider as it passes from the base to the summit of the cochlea. The length of the rods also increases towards the summit of the organ, their bases being more widely separated from one another and their point of junction nearer to the basilar membrane, this forming a lower and wider tunnel. The number of rods of Corti has been estimated at 6,000 inner, and 4,500 outer.

Stimulation of the Auditory Nerve.

The stimulation of the nerve of hearing by sound-vibrations of the air is less difficult to understand than the excitation of the optic nerve by light-waves which are conveyed by an imponderable medium. The motions of the membrane of the drum, being conveyed in the manner already indicated to the liquids within the internal ear, pass over and under the cells connected with the nerve terminals, which are placed on the elastic basilar membrane. The transverse fibres are set in motion by the waves in the fluid, and as they vibrate they communicate the motion to the organ of Corti. The bases of the inner rods, being fixed at the inner margin of the basilar membrane, can move but little, and the bases of the outer rods being placed near the middle of the fibres of the membrane, where the motion of the vibrations is most extensive, a slight change in their relative positions, and a consequent movement of the apex of the bow takes place. This movement at the apex of the bow, where the rods join, is communicated by the medium of the reticular membrane to the hairs in the special auditory cells, thence to the nerves, where an excitation is produced giving rise to the transmission of an impulse to the brain.

We can distinguish differences of (1) loudness, (2) pitch, and (3) quality in sounds.

Since the *loudness* depends simply on the amplitude of the vibration, we have no difficulty in understanding how variations in it can be appreciated, since the more ample the vibration the more marked the motion, and, therefore, the more intense the stimulation of the nerve terminals. What we call the loudness of a sound simply means greater or less intensity of stimulation of the nerve.

The perception of difference of *pitch* presents greater difficulty. As already mentioned, this depends on the rate of vibrations. We know that most bodies capable of producing sound vibrations have a proper tone, *i.e.*, that which they produce when struck. When the tone proper to a body capable of vibrating is sounded in its immediate neighbourhood, it also is set vibrating through the medium of the air. If a clear tone be sung loudly over the strings of a piano a kind of sympathetic echo will be heard to come from the strings corresponding to the notes sounded. In the basilar membrane we have practically a series of strings of different length—since the membrane gets wider as it passes from below upwards to the summit of the cochlea—and therefore a great variety of proper tones. With a high note a fibre of one part of the membrane will readily fall into vibration, and with a low note a fibre of another part. Different nerve fibrils are in relation to these different parts, and we may conclude that tones of different pitch stimulate distinct nerve-terminals, and are conveyed to the brain by separate nerve-channels. Impulses arriving at certain brain-cells give rise to the idea of high tones, and impulses coming to others cause the impression of low tones. There are about a sufficient number of fibres in the basilar membrane for all the notes we can hear, viz., from about 33 to 38,000 waves in the second.

The rods of Corti cannot be the vibrating agents, because they are absent in birds which appreciate and reproduce various notes ; and they are too few for the notes we hear. Further, the rods are not elastic, and not well suited for vibration. It may therefore be concluded that they only act as levers which convey the vibrations of the fibres of the basilar membrane to the nerve-endings in the auditory cells.

The explanation of our wonderful appreciation of the delicate shades of *quality* of tone is still more difficult. Even persons with indifferently good ears, as musicians say, and no special musical education, can at once distinguish between the quality of the same note when sounded on a violin, a piano, and a flute. When a note is sung against the strings of a piano, however pure its tone, a great number of strings are set vibrating. Not only does the string of that note vibrate, but also all those that have a certain simple numerical

relation to its vibrations. In fact, all its over-tones resound. In the cochlea we suppose the same to take place with the fibres of the basilar membrane. Not only does the one fibre whose proper tone is sounded vibrate in response, but also all those which represent the varied over-tones or harmonics. It has already been pointed out that the *quality* of a tone depends on the relative number, force, and arrangement of harmonics, which invariably accompany any musical note that possesses a definite character.

When a note arrives at the auditory nerve-terminals, one of these is strongly stimulated by the wave of the fundamental tone, and many others by the different over-tones, for every prominent over-tone stimulates the cochlea. The complexity of the impression increases with the impurity of the tone, and so we appreciate the quality of a note. Thus, a compound of impulses, corresponding to a mixture of tones of varying intricacy, is transmitted to the brain-cells, where it gives rise to the impression of the quality which we by experience associate with that of a violin, flute, or piano, as the case may be.

With regard to the judgment of the distance of sound, it need only be remarked that it chiefly depends on former experience of the habitual quality and intensity of sound. A faint sound with the same quality that we familiarly attribute to loud sound seems to us to be far away. Thus, sounds reaching our labyrinths by the cranial bones appear distant, and ventriloquists deceive us by imitating the character of distant sounds.

The direction from which sound comes is chiefly judged by the difference of intensity with which it is heard by one or other ear. When we cannot form any idea of whence a sound comes we turn our heads one way or the other in order to present one ear more directly to the origin of the sound. When a sound is either directly behind or before us we cannot judge from which position it really comes, unless the head be slightly turned to one side or the other before the vibrations have ceased to be audible.

CHAPTER XXXIV.

CENTRAL NERVOUS ORGANS.

THE central part of the nervous system, or *cerebrospinal axis*, consists of the spinal cord, the medulla oblongata, and the brain.

The central nervous organs are composed of a soft texture, consisting of nerve-cells and nerve-fibres, held together by a peculiar and

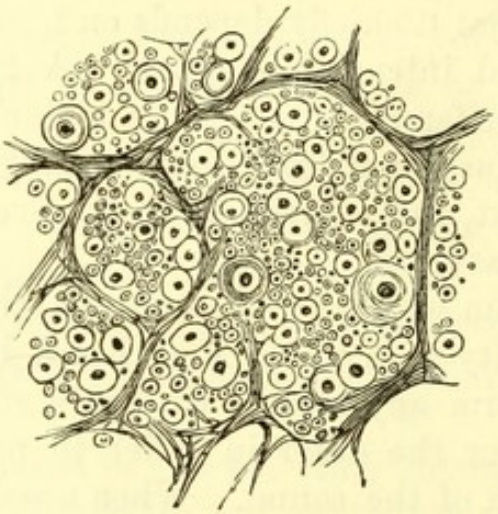


Fig. 239.—Transverse section of nerve fibres, showing the axis cylinders cut across, and looking like dots surrounded by a clear zone, which is the medullary sheath. Fine connective tissue, in connection with neuroglia, binds the fibres into bundles.

very delicate form of connective tissue, known as *Neuroglia*. With the naked eye the central nervous organs can be seen to be composed of two distinct kinds of substance: (1) *a white substance*, found by the microscope to be composed of nerve fibres, with a medullary sheath, and (2) *a grey substance*, consisting of a dense feltwork of naked axis cylinders, with numerous ganglion cells interspersed between them.

In the brain the grey substance is distributed chiefly on the surface, forming a kind of grey *cortex*, which follows all the irregularities of the convolutions.

In the spinal cord the grey matter is situated inside, and the white outside. If viewed longitudinally the grey substance of the cord forms separate columns on either side, which extend throughout its entire length and are thicker in the cervical and lumbar regions. These

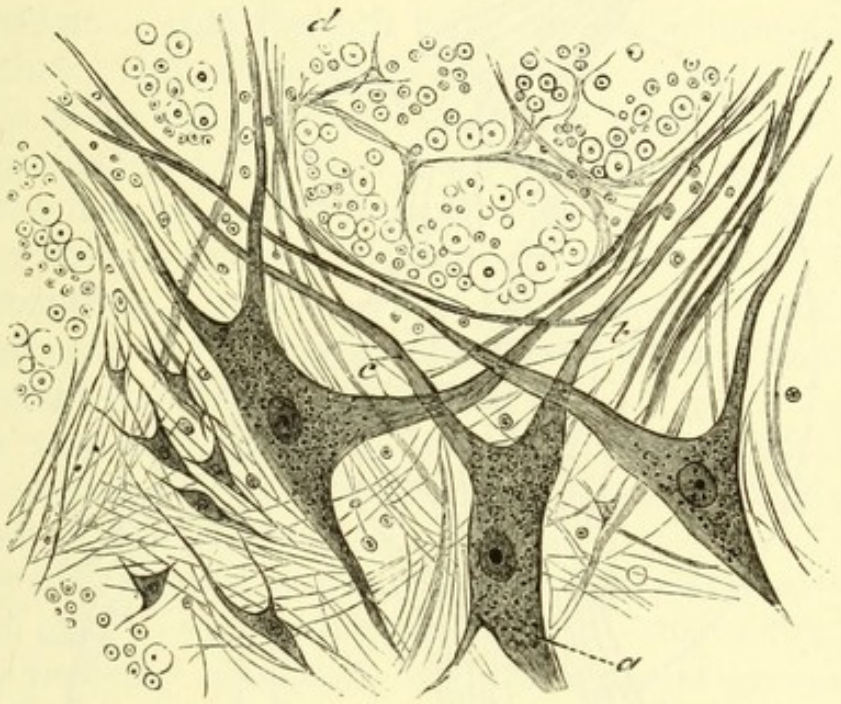


Fig. 240.—Multipolar cells from the anterior grey column of the spinal cord of the dog-fish (*a*) lying in a texture of fibrils; (*b*) prolongation from cells; (*c*) nerve-fibres cut across. (Cadiat.)

grey columns, together with their connections with the roots of the spinal nerves, divide the white substance of the cord into more or less distinct regions called the posterior and antero-lateral white columns.

The general properties of the elements of nervous tissue have been described in Chapter XXVIII. The functions there enumerated belong also to the fibres and cells of the cerebro-spinal axis, and therefore require no further general description here.

Besides having the power of *conducting*, *reflecting*, *co-ordinating*, *inhibiting*, *retaining*, and *originating* impulses, we must attribute to the activity of the nerve-cells of the brain the various mental phenomena, such as feeling, thought, volition, memory, &c., which forms of activity may be excited either by impulses arriving from without, or by the automatic action of the cells of the cerebral cortex.

The Spinal Cord.

The Spinal Cord being the great bond of connection between the brain and the majority of the peripheral nerves, is necessarily a

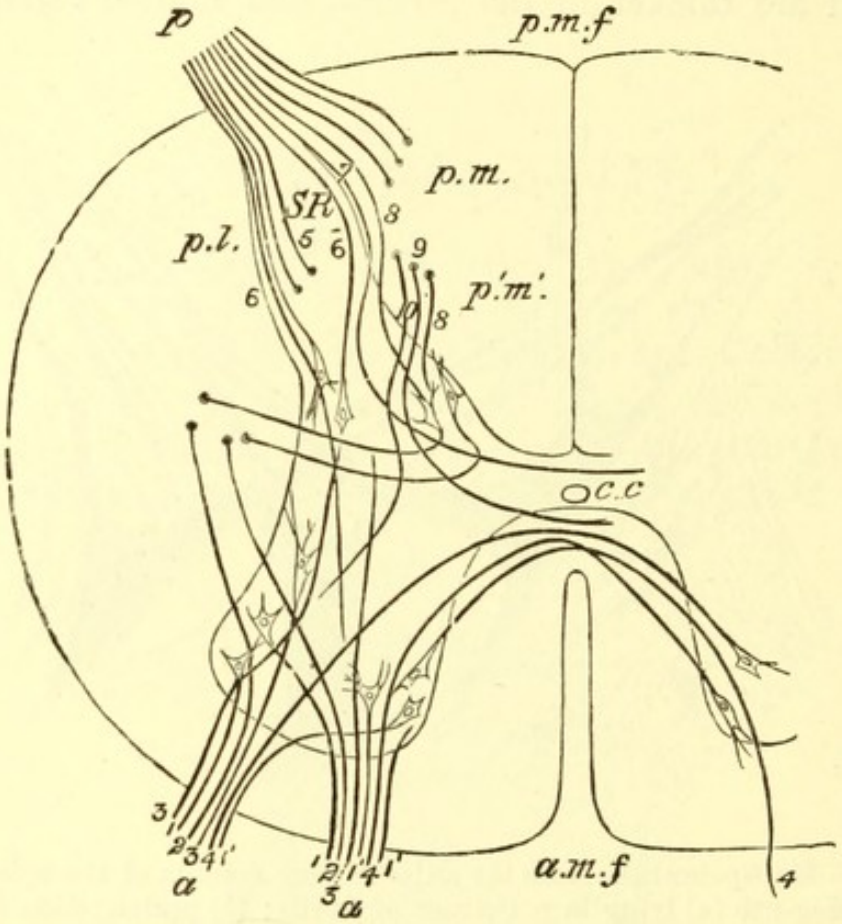


Fig. 241.—Diagram illustrating the paths probably taken by the fibres of the nerve-roots on entering the spinal cord. (Schäfer.)

a.m.f., Anterior median fissure; *p.m.f.*, Posterior median fissure; *c.c.*, Central canal; *s.r.*, Substantia gelatinosa of Rolando; *a.a.*, Funiculi of anterior root of a nerve; *p.*, Funiculus of posterior root of a nerve. By following the fibres 1, 2, 3, &c., their course through the grey matter of the spinal cord may be traced.

conducting apparatus of the very first importance, and from the quantity of nerve-cells lying in its grey matter, it must also exercise the function of a governing organ, or *nerve centre.*

I.—Spinal Cord as a Conductor.

Anatomical methods.—Anatomical investigation shows that the spinal cord is not merely a collection or aggregation of the fibres that pass into it. In the first place, the spinal nerves, if bundled together, would be much larger than the cord, even at its thickest

part; and secondly it does not taper evenly towards its lower extremity, as it should were each succeeding pair of roots a direct loss of thickness. The question then arises how are the fibres of the spinal nerves disposed of in the cord.

The *posterior roots* of the spinal nerves (Fig. 241, *p*) pass through the white substance to reach the posterior grey column (*SR*), where they break up into twigs, some of which are distributed to neighbouring parts of the grey network of fibrils, in which they are lost without their union with the cells being obvious or immediate, while others pass into the posterior white columns.

The fibres of the *anterior roots*, in irregular bundles (*a*, *a*), traverse the superficial white part of the cord on their way to reach the anterior grey columns, into the cells of which some can be directly traced; others enter the grey matter without joining the cells. The other processes from these cells pass into the fibrillar network which makes up the great mass of the grey substance, and are in communication with the distant parts of the cord above.

Anatomy may thus be said to leave us in the dark in regard to the paths traversed in the cord by the impulses on their way to or from the root of the spinal nerves.

Histology only teaches us that the grey and white matter of the cord consist of—(1.) Innumerable fibrils and cells, and (2.) Medullated fibres variously connected with the different groups of cells and the roots of the spinal nerves.

Since ordinary histological research fails to show the complex connections of the fibres of the spinal cord, other methods have been resorted to in attempting to discover their course. Of these the two following have given good results :—

Developmental method.—It was found that the medullary sheath of the fibres in different white tracts of the cord was perfected at different ages of an animal, and by tracing the course of the imperfectly developed fibres the functional relations of certain tracts could be arrived at.

Degenerative method.—It is well known that a degenerative process (sclerosis), easily recognised histologically, soon follows the section of nerve-fibres. This change takes place first in those fibres situated at the side of the section towards which the impulses travel; *i.e.*, at the peripheral end of an efferent and central end of an afferent fibre. By carefully tracing the course of the degenerated tracts after section or pathological lesion the function of the fibres and their connections with other parts of the nervous centres can be determined.

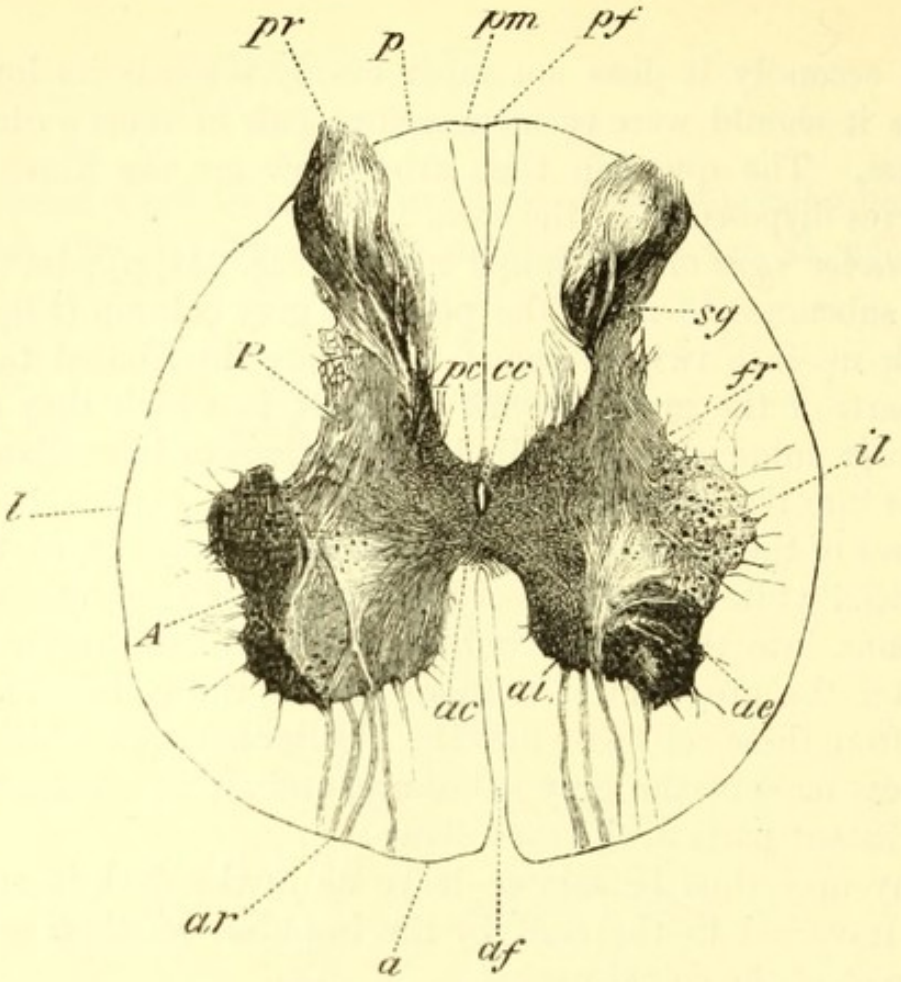


Fig. 242.—Transverse section of the *lumbar region* of the spinal cord (for reference see description under Fig. 244). (Bevan Lewis.)

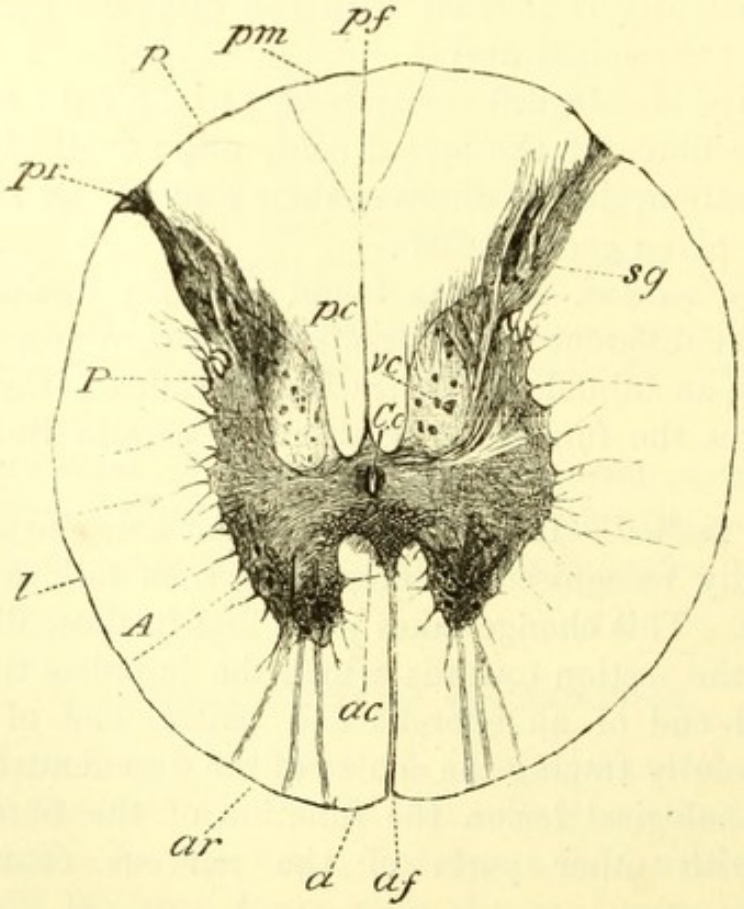


Fig. 243.—Transverse section of the *dorsal region* of the spinal cord. (Bevan Lewis.)

By these methods the following tracts of white fibres have been made out in the spinal cord :—

1. The *direct pyramidal tracts* (Türk) (Fig. 245, T), each of which is continuous with the pyramid on the *same side* of the medulla

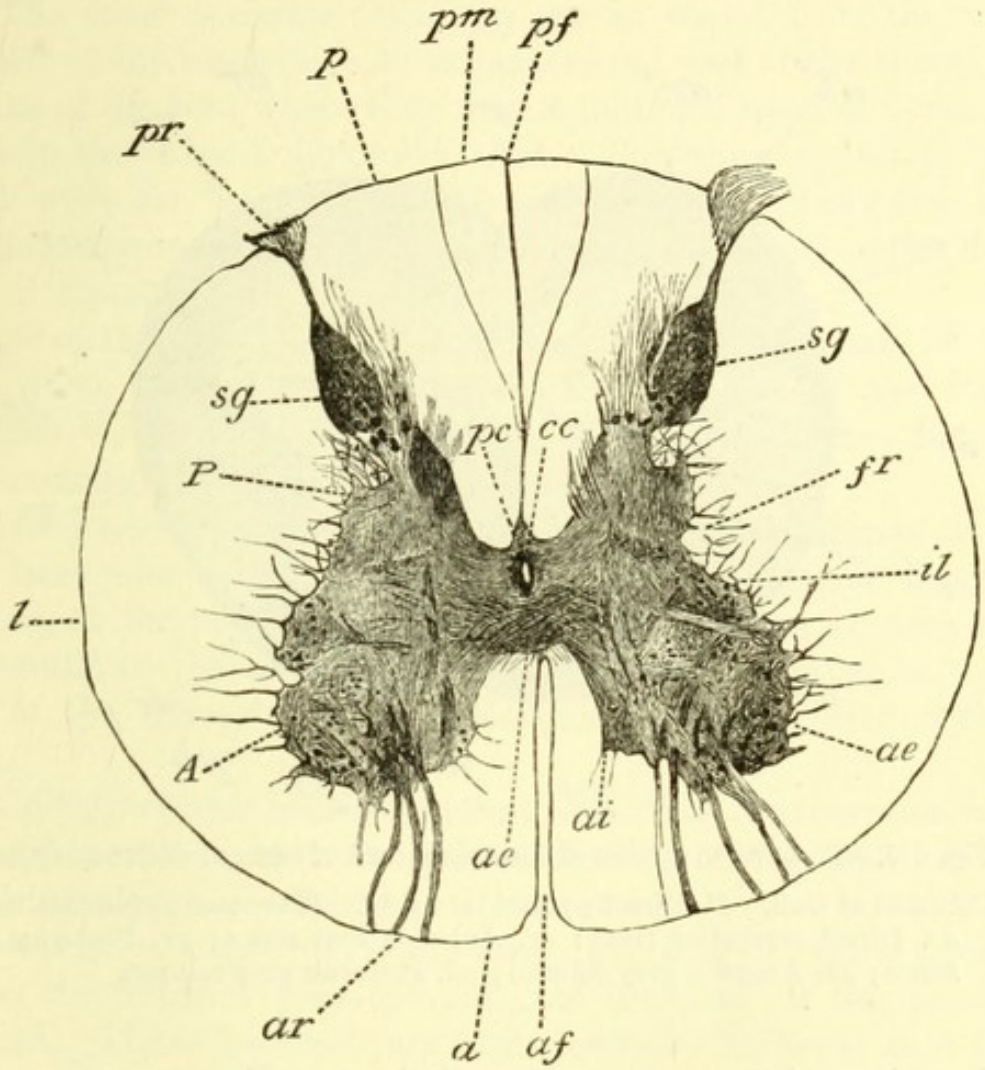


Fig. 244.—Transverse section of the *cervical region* of the spinal cord.

A. Anterior grey column.
a. Anterior white column.
l. Lateral white column.
ac. Anterior commissure.
ar. Anterior roots.
af. Anterior median fissure.
il. Intermedio-lateral grey column.
vc. Vesicular column of Clarke.
P. Posterior grey column.
p. Posterior white column.
pm. Posterior median column.
pc. Posterior commissure.
cc. Central canal.
pr. Posterior roots.
pf. Posterior median fissure.
ae and *ai*. External and internal anterior vesicular columns.
sg. Substantia gelatinosa.

oblongata. They lie on the inner aspect of the anterior white column, and form the immediate boundaries of the anterior median fissure. These tracts taper from above downwards to nothing, and terminate about the middle of the dorsal region. The fibres leaving

them appear to cross by the anterior commissure to reach the anterior grey column of the opposite side.

2. The *crossed or lateral pyramidal tracts* (Fig. 245, P) are continuous with the pyramids of the *opposite side* of the medulla where the crossing of the fibres is completed. They lie in the

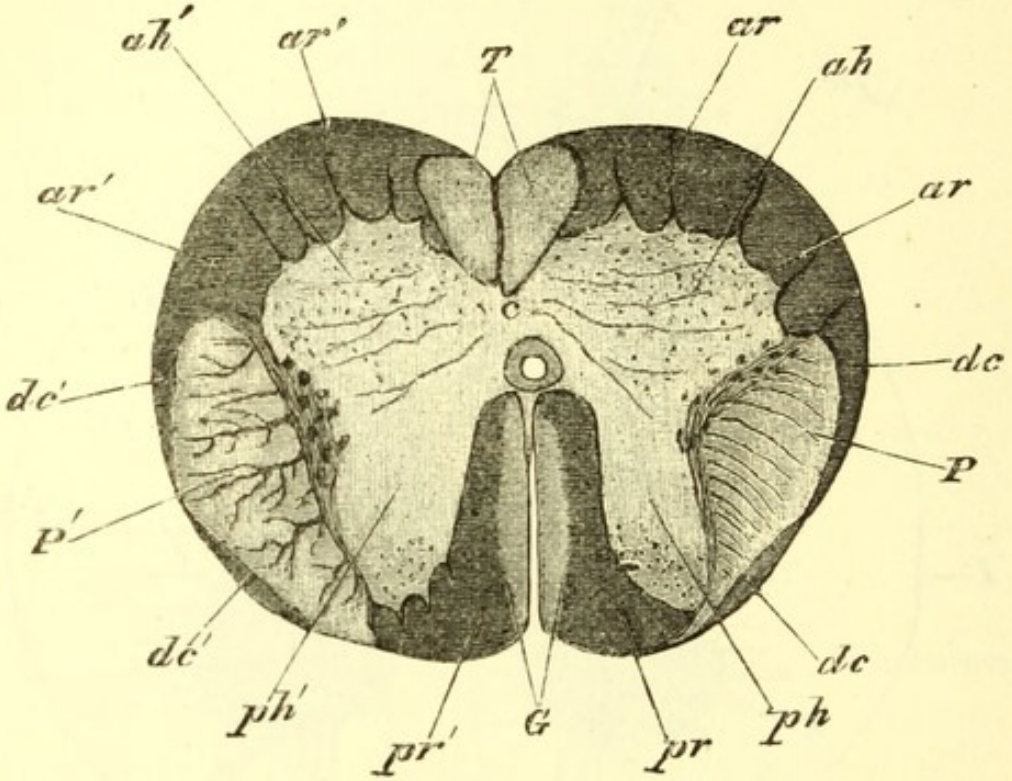


Fig. 245.—Transverse section of the spinal cord of embryo at five months.

G. Columns of Goll. *T*. Direct pyramidal tracts. *P*. Crossed pyramidal tracts. *dc*. Direct cerebellar tract; *ar*. Anterior root zones; *pr*. Posterior root zones; *ah*. Anterior grey column; *ph*. Posterior grey column.

lateral white columns, occupying their posterior part next to the posterior grey columns, and are separated from the surface by the direct cerebellar tract (*dc*). The crossed pyramidal tracts also taper towards the lower part of the cord, but can be traced to the lumbar region. The fibres are connected with the anterior grey column of the same side.

Section of these tracts in the cord of the pyramids in the medulla, or the channels leading from the motor areas, as well as destruction of the motor areas in the cortex of the brain, is followed by descending degeneration of both these pyramidal white columns along their entire extent. The track of degeneration corresponds with the limits assigned by developmental research to these pyramidal tracts. It therefore seems clear that they are the channels by which the efferent impulses from the brain travel to the cells of the anterior

cellular column of the spinal cord. There seems to be no functional difference between those fibres that cross in the medulla at the decussation of the pyramids, and those which pass directly from the medulla to the same side of the cord, and then gradually cross on their way to their destination.

3. The *direct cerebellar tracts* (*dc*) can be traced from the inferior peduncle of the cerebellum to the superficial part of the lateral white columns of the cord where they form a flattened band of fibres which covers in the crossed pyramidal tract. The fibres appear to be connected with the cells of Clarke's column, to be described below. This tract tapers towards the lumbar region about the upper limit of which it disappears.

After section of the cord ascending degeneration can be traced along these tracts through the restiform bodies of the medulla oblongata to the vermiform process of the cerebellum. Hence we may conclude that they carry centripetal impulses.

4. The *posterior median columns* (Goll) are thick strands of white fibres, triangular in section (Fig. 245, G), which form the immediate boundary of the posterior median fissure. They can be traced from the medulla to the mid-dorsal region, where they taper to a point. Some of the fibres of the posterior roots are connected with this column.

In Goll's posterior median column ascending degeneration can be traced, after section, up to the clavate nucleus of the medulla. This tract is therefore also afferent.

5. *Anterior root zone* (*ar*) is the name given to the white substance next to the anterior grey columns not included in the parts just described. These tracts do not taper towards the lower part of the cord, but vary in thickness with that of the roots of the spinal nerves, being thickest at the cervical and lumbar enlargements.

After transverse section of the cord descending sclerosis can be traced a short distance down these tracts. The direction of the degeneration shows them to be efferent, but from the limited extent of the sclerosis we may suppose that they only carry impulses from the upper to the lower regions of the spinal cord.

6. *Posterior root zones* (Burdach) (*pr*) surround the part of the grey column from which the posterior roots spring and vary in proportion to the size of the roots of the spinal nerves.

The mode of degeneration (limited ascending sclerosis) of these fibres teaches us that they are afferent channels probably carrying impulses from the cells of the lower parts of the posterior grey columns to those in its upper segments.

Experimental methods.—Besides the foregoing anatomical facts, we learn from experimental research certain facts concerning the loss of function which follows transverse sections of different extent, of the spinal cord.

1. Complete section of the cord is followed by loss of sensation and

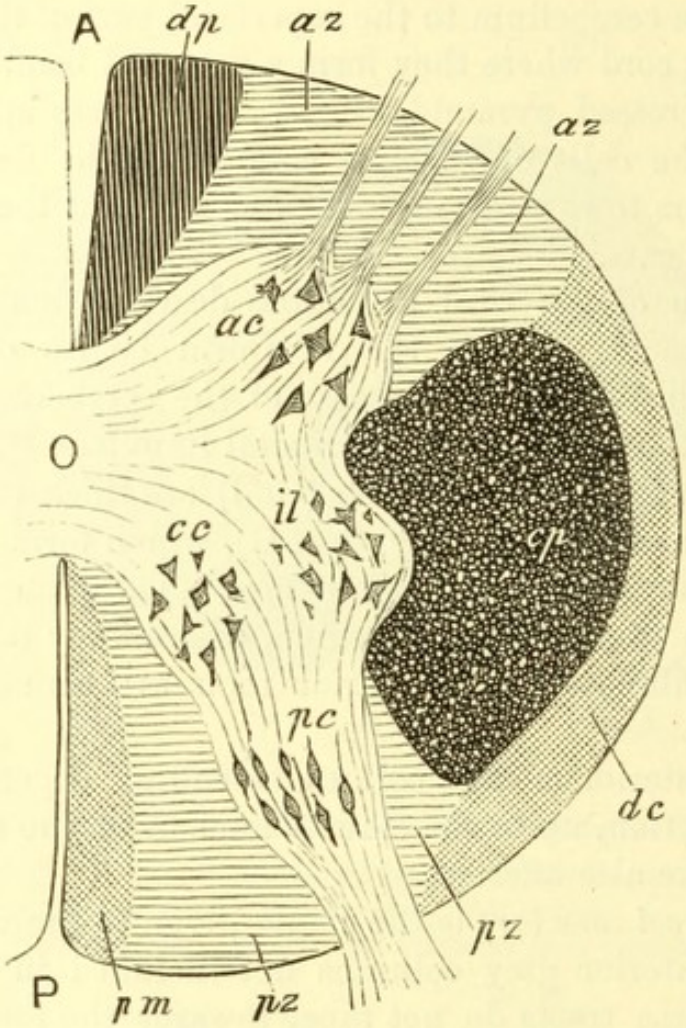


Fig. 246.—Diagram of transverse section of the cervical parts of the spinal cord, showing the white tracts supposed to be functionally distinct by differences of shading.

A. Anterior; P. Posterior median fissures. *dp*. Direct pyramidal; *cp*. Crossed pyramidal tracts; *dc*. Direct cerebellar; *pm*. posterior median column (Goll); *az*. Anterior; *pz*. Posterior root zones.

the power of voluntary motion in the parts below the point of section (Galen).

2. Section of one side of the cord is followed by loss of sensation on the side of the body opposite to and below the section, and loss of all voluntary motion of the parts below and on the same side as the injury of the cord. Increased sensitiveness of the parts where the motor paralysis exists is also said to be observed in some of the lower animals.

3. If the grey matter and the anterior and posterior white

columns of one half of the cord be cut across, *i.e.*, when only the lateral white columns remain intact on that side. Both motor and

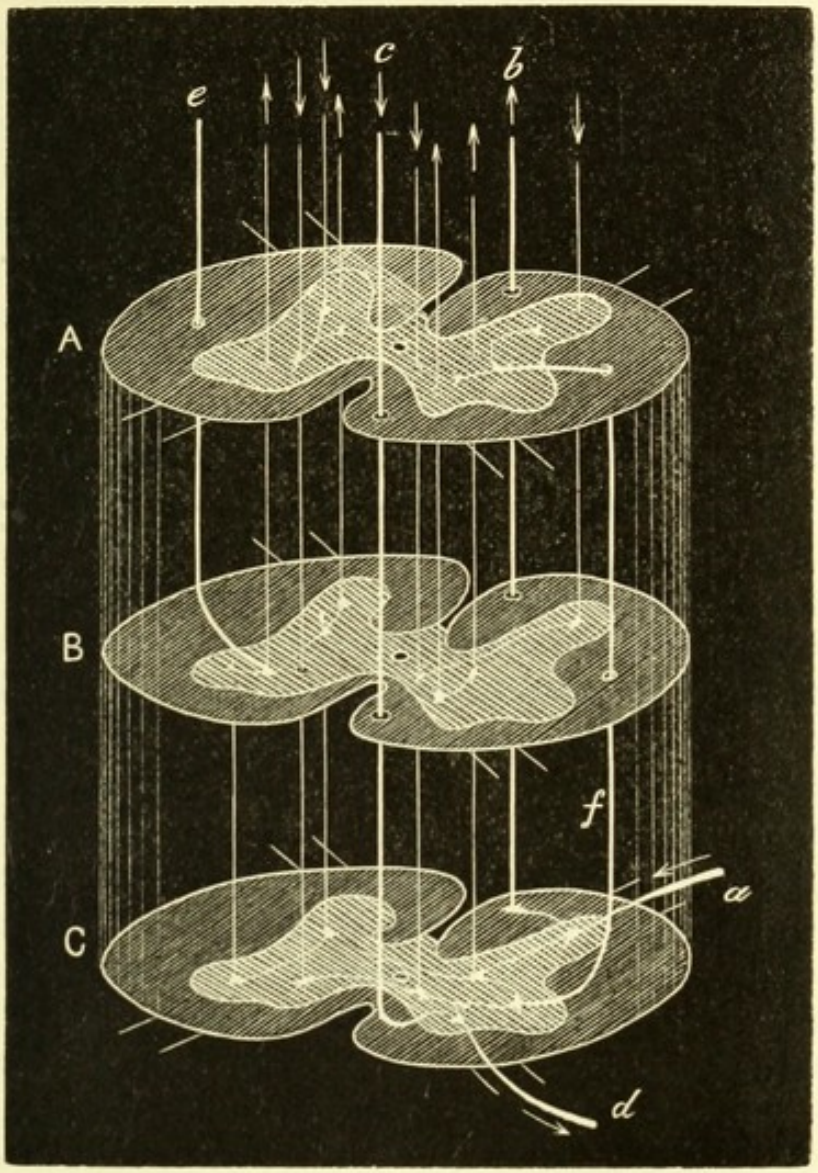


Fig. 247.—Diagram illustrating the course taken by the fibres in the spinal cord. (After Fick.)

A, B, and C represent oblique transverse sections of the cord, the tissue between being supposed to be transparent. At the lowest section (C), sensory nerve fibres (*a*) enter by the posterior root, and are connected with ganglion cells of the grey matter, and, through the posterior white column, with the brain (*b*).

Impulses arriving by the same posterior root may, to reach other parts, traverse the finer fibrils of the grey matter—shown by the fine lines.

When an impulse comes directly from the brain (voluntary centres) it adopts the direct routes (*c* or *e*), passing through the pyramidal tracts, to excite the motor ganglion cells of the cord to co-ordinated activity.

From many parts of the grey matter ganglion cells despatch impulses by the motor root (*d*)

Some white fibres only communicate between the cells of the various segments of the grey matter (*f*).

sensory impulses (as observed in the rabbit) seem to be transmitted normally.

4. Longitudinal section of the commissures which unite the two sides of the cord, so as to separate the lateral halves, is said not to influence voluntary motion, but produce an ill-defined loss of sensation below the lesion.

5. Experiments consisting of partial and local sections were conducted with the object of determining the exact course of the impulses giving rise to different kinds of sensation; and it was concluded that ordinary sensory impulses (pain) travelled by the grey matter, while tactile temperature and muscle sense travelled *viâ* the posterior white columns. Though pathological observation and the occurrence of "analgesia" (unimpaired tactile sense with local loss of painful impressions) suggest the idea of such distinct paths for different kinds of sensation, it would appear that the localization of pain to the grey matter and of touch, &c., to the posterior white column cannot be accepted as demonstrated experimentally.

From the foregoing we may draw the following conclusions :—

1. Voluntary motor impulses from the cortex of the brain travel directly to the pyramidal tracts, and thence to the cells of the anterior grey columns. The fibres decussate in the medulla or in the upper part of the cord.

2. Motor impulses travel from the upper to the lower segments of the cord in the white fibres around the anterior grey columns.

3. Various afferent impulses cross at once on entering the cord to the posterior grey columns of the other side, and then ascend by the neighbouring white fibres of the posterior root zones, the direct cerebellar tract, the posterior median tract of Goll, and probably also by some of the white channels of the lateral column.

4. Besides their numerous thin protoplasmic connections in the various segments of the grey matter, all the cells of the cord are in communication with their more distant neighbours by means of the white fibres of the root zones.

Spinal Cord as a Collection of Nerve Centres.

In the grey substance there is still greater difficulty in tracing the course taken by the various kinds of impulses, and little is known on the subject beyond what is surmised from the proximity of the different parts to the anterior and posterior roots and to the white channels the function of which is known.

Though the attempt to localize the different functions to any anatomical region has not met with success, histology has taught

us of the existence of certain groups of cells which when viewed longitudinally may be called *vesicular columns*. Of these four may be named as distinctively marked. (Fig. 246.)

1. The *anterior* (motor) *cellular columns* occupy the grey matter seen in sections of the cord as the anterior cornua. They extend throughout the entire length of the cord, the cells being specially numerous where the large motor roots come off. The cells are characterised by their great size and the number of their branches, one of which forms the axis-cylinder of one of the motor fibres passing to the roots of the spinal nerves.

2. The *posterior cellular columns* situated in the grey matter of the posterior cornua are much less obvious than the anterior. The cells are few, small, and mostly spindle-shaped. Their processes are not readily traced to the roots of the spinal nerves.

3. The *postero-median cellular column* (Clarke) lies on the median side of the posterior grey column, so that it forms the inner part of the posterior cornua near its base. The cells are numerous, but much smaller than those of the anterior vesicular column. Clarke's column is best developed at the junction of the lower dorsal and upper lumbar nerves. It tapers off above and below, and the cells cease to form a continuous column opposite the seventh cervical nerve. But scattered groups of cells in a corresponding position are found throughout all the cervical cord, and seem to link this spinal column with the vagus nucleus in the medulla.

4. The *intermedio-lateral cellular columns* lie in the lateral concavities seen on section between the anterior and posterior grey cornua. They thus occupy a position between the lateral white column and the central part of the grey matter. They are best marked in the dorsal region, as they seem fused with the cells of the anterior cornua in the lumbar and cervical enlargements.

The facts that cells functionally related are grouped in masses at the points where the spinal nerves arise, and that the various regions of the cord can respond to stimulus when severed from the rest, seem to indicate that a strict homology exists between the spinal centres of vertebrate and the central nervous system in many of the lower animals, which consists of a double chain of ganglia, united together by conducting channels.

We may then suppose the grey matter of the spinal cord to be made up of a series of segments, corresponding in number to the vertebral development, fused together into one continuous organ. These segments may be supposed to receive the afferent impulses from corresponding parts of the body, and send efferent impulses to

muscles capable of moving that part, just as the separate ganglia of the invertebrate chain preside over the functions of the corresponding somite of the animal's body.

The various groups of cells in the spinal cord are in more or less direct union with the roots of the nerves, and the conducting fibrils of the cord itself, so that they participate in the transmission of the impulses to and from the centres situated in the brain. In the transmission of these impulses the cells seem to have a certain directing and controlling influence which deserves special attention, as it gives us the key to the more complex mechanisms of the higher centres. Although the various powers exerted by the cells of the spinal cord are so intimately associated together as to be practically inseparable, it is found convenient to consider their functions under distinct headings.

Reflex Action.

When an afferent impulse arrives at the cells of the posterior column, it is communicated to the cells in the same segment, and reaching motor cells it gives rise to a movement of the muscles of the neighbourhood from which the impulse first started. At the same time impulses travel to the brain, and there give rise to a consciousness of the various events taking place, *i.e.*, a local stimulation and a local movement. The action of the cells of the cord takes place without the aid of the will, and occurs before the mind is conscious of it. These movements, being a turning back of the impulse, are called *reflex acts.*

Reflex action forms the most ordinary function of the cells of the spinal cord. Even the gentlest stimulation may give rise to a complex movement, the execution of which requires many muscles to act together, as it were, with a common object. An unexpected touch to the finger causes a person to withdraw the hand quickly. If greater or more prolonged stimulus be applied, more extensive movements occur, by the well-arranged co-operation of many muscles, a forcible, definite and familiar action is performed. For example, if the burning head of a match adhere under the thumb-nail, more than a mere withdrawal of the hand takes place. The entire arm is violently shaken, before the will has time to come into operation. We have here a complex form of purposeful muscular movement, the immediate result of an impulse coming from a single point of the skin, owing to the spreading of the impulse to the cells of the segments in the vicinity. The movement is regular,

performed with a definite purpose, as if it were the result of thought, but since there is no consciousness, it cannot be mental.

If the degree of stimulation be carefully regulated, it will be found that the results obtained by peripheral stimulation depend on (*a*) the strength of the stimulus, and the length of time for which it is applied; (*b*) the degree of excitability of the cells, and the readiness with which the impulses pass along the thin conducting channels to the grey matter, and (*c*) the functional activity of the muscles which act as indicators of the reflex effects.

All these points may be easily studied on a frog decapitated about an hour beforehand. If the animal be suspended by the lower jaw, and the toe touched, the foot is gently withdrawn. If the toe be smartly pinched, the entire limb is forcibly raised; with intense or prolonged stimulus both legs are violently moved. If a fragment of blotting-paper, moistened in weak acid, be placed on the belly, in a position not easily reached by the foot, a complex series of movements follows. The muscular action is both elaborate and purposeful, and the movements of the headless animal might almost be called ingenious.

Strength and duration of stimulus.—By graduating the *strength* of the acid used to moisten a square millimetre of blotting paper, the following results are obtained. When very weak acid is employed only slight local and uni-lateral movement is caused. Stronger acid produces a series of reflex movements, spreading to several muscles on both sides of the body. If further strengthened, the movements become violent and more extended until the whole body is thrown into convulsion. The movements spread from the nerve cells to their neighbours, and then to those governing the corresponding muscles of the other side, in which, however, they are less marked than in those of the side stimulated.

Slight stimulation, when of short duration, not sufficient to produce immediate response, may, after a time, give rise to definite reflex action, as if the weak impulses arriving at the nerve-cells in the cord were stored up until their sum sufficed to produce a definite reflex movement. This may be seen in animals whose nerve centres are intact, for the cells of more remote parts exercise a kind of checking influence on those in the region receiving the stimulus and thus the accumulative action (summation) comes more effectively into play. In the human subject, where slight visceral stimulations exist for a long time, this summation may be observed. In some of these cases, even without sensory appreciation of the local excitation, an amount of energy may be accumulated in the

grey tracts of the cord, that will bring on the most extensive forms of reflex muscular movement. These movements differ often from the regular co-ordinated motion resulting at once from skin stimulation. As an example of this may be named the convulsions that occur in young children, from the prolonged irritation of intestinal worms, or during the painful period of dentition.

Exalted excitability of the cells.—In certain conditions of the nervous system convulsions can be readily excited. As most striking among these, may be named poisoning with the alkaloid of nux vomica (strychnia), and the state of the blood which is produced by cessation of the respiratory function (asphyxia). These toxic conditions bring about a peculiar excitable state of the cells or conducting fibres of the spinal cord, in which impulses pass with unwonted facility from one part to another, and give rise to an excessive degree of action even in response to gentle stimulations. A frog poisoned with strychnia is thrown into general spasm by the least touch, which normally would only cause it to withdraw the limb.

On the other hand, there are many *poisons* which deaden the reflex powers of the cord centres, among which are opium, chloroform, chloral, digitalin, &c. The condition of the blood (*apnœa*) which may be brought about by very rapid movements during artificial respiration, has also the effect of lowering the excitability of the spinal nerve-cells, and slowing respiration.

Inhibition of Reflex Action.

The great majority of reflex actions may be prevented orcontrolled by the *will*, and the *basal ganglia* and *medulla* habitually exert a checking or inhibitory influence on the reflex actions of the spinal cord. It is in this way that we account for the facts that a living frog when stimulated does not respond with the ordinary reflex movements, and that a human being, when asleep, shows reflex action in response to a slight stimulus that would be quite ineffectual were he awake. For some little time after pithing a frog, constant or regular results are seldom met with, because the section of the upper part of the spinal cord acts as a stimulus to those channels which habitually bear impulses from the brain, and, by exciting them, has inhibitory effect. Further, artificial stimulation of the *corpora quadrigemina* and medulla have the effect of checking the reflex action of the cord.

If, while the cord is employed in reflex action, in response to gentle cutaneous stimulation, the central end of a large *sensory nerve* trunk be stimulated, the reflex action ceases. In short, it may be accepted that strong impulses arriving at the cord from any direction, have the effect of inhibiting the action of its reflecting cells.

The theory of reflex action lies at the bottom of all nervous activities, and it is therefore useful to attempt to work out the details of the mechanisms by means of which it is carried on. A simple plan of the channels traversed by the impulses is given in the diagram (Fig. 248), in which the arrow-heads show the direction of the afferent impulse passing along the posterior root to reach a cell in the posterior grey column, thence it passes to a cell in the anterior column, to reach the efferent fibre, and through the anterior motor root of the nerve on its way to the muscle. It has been suggested that the impulse meets with considerable resistance in passing through the protoplasm of the cells, and that owing to this resistance, the effect of a slight stimulus remains localized, while more powerful impulses can overcome the resistance, and spread to a greater number of cells. Thus the regular radiation in the cord would be simply dependent on the inability of the impulses to affect cells other than those in their immediate neighbourhood. Following out this view, it has been suggested that the resistance is increased by impulses arriving at the cells from a different direction, and the inhibitory action of the higher centres, or peripheral excitation of another part, impedes the spreading of the impulses.

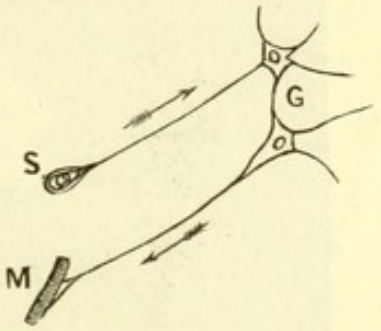


Fig. 248.

S. Sensory receiving organ with attached afferent nerve fibre.
G. Central organs—ganglion cells.
M. Peripheral organ and efferent nerve.

But this theory of *resistance* to, and *interference* with the transmission of impulses in the nerve-cells hardly explains all the phenomena observed in the reflex action of the spinal cord and the various modifications it can undergo.

The reflex convulsions that occur in poisoning with strychnin, or as the result of some constant but slight stimulation, may be explained as follows.

Besides the resistant protoplasmic fibrils in the grey part of the cord, there exist medullated fibres in the root zones—short cuts, as

it were—by which impulses travel from one part of the cord to another. If we suppose the ordinary reflex traffic of the cord-cells

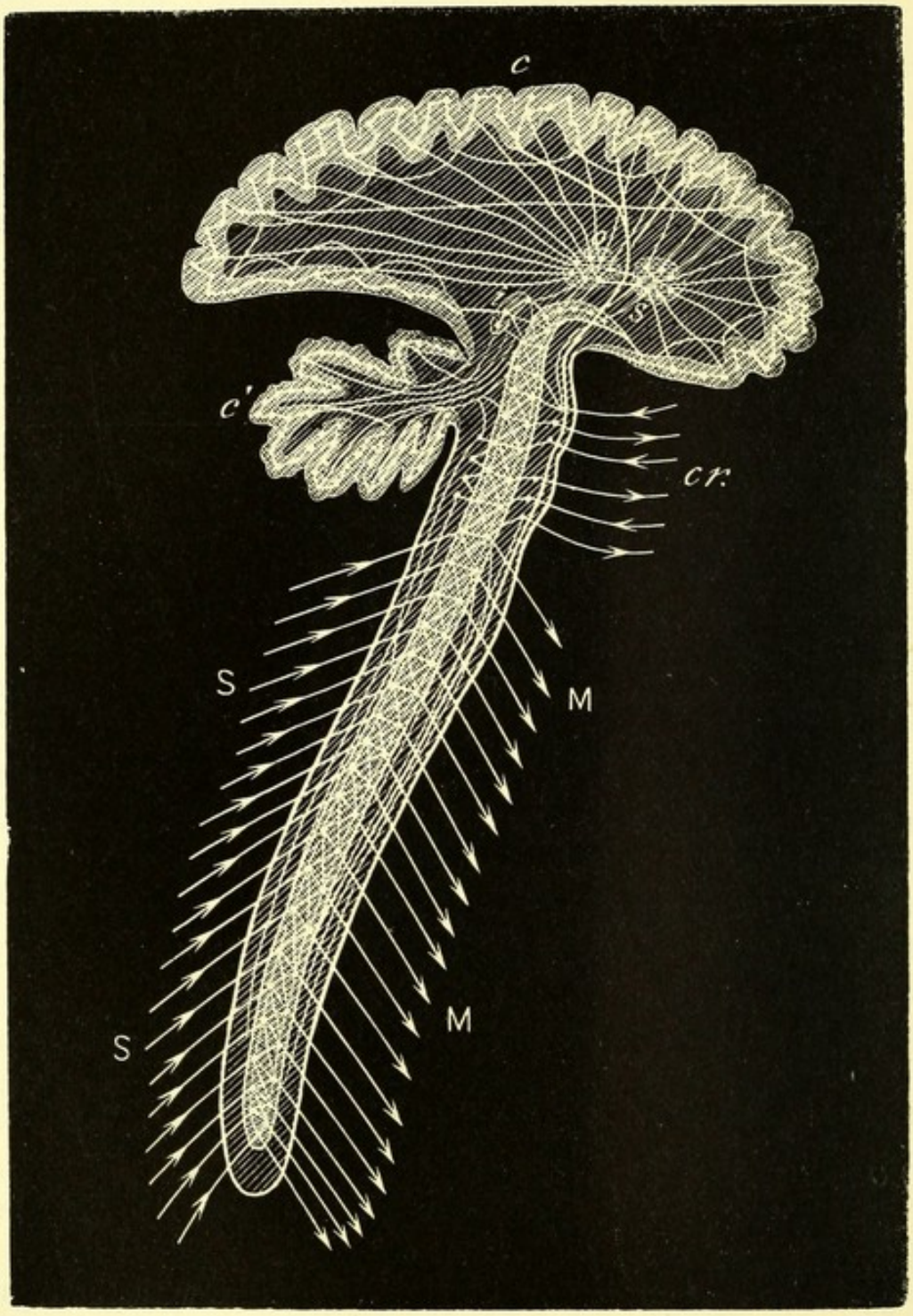


Fig. 249.—Diagram of the paths taken by the impulses in the brain and cord. MM., motor channels; SS., sensory channels; CR., cranial nerves.

to be carried on without the assistance of these direct lines of communication, we must assume that there is some special means of shutting these fibres out of the working of the reflex machine. Such special mechanisms in all probability exist, and are in relationship

with, or under the command of the inhibitory cells of the higher centres. We may then suppose that strychnin removes the power of these inhibitory agents, and the impulses finding the direct ways open, take these routes, and are simultaneously and irregularly diffused throughout all the cell-territories (independent of the ordinary paths they have been educated to follow), and thus convulsive movements are excited in many parts of the body.

In like manner the unremitting activity necessary to keep in check the impulses arriving from a constant source of stimulation (such as intestinal worms), eventually fatigues the active elements in this inhibitory mechanism, and then—often suddenly—the force of the accumulated irritation rushes along the direct channels to all parts of the cord, and simultaneously exciting them, brings many discordant muscles into spasmodic action.

The reflexion of an impulse from a sensory nerve, through the cells of the spinal cord to a motor nerve, occupies a measurable length of time, which has been estimated at about $\frac{1}{10}$ of a second. The time required for the performance of a reflex act varies considerably in the same individual under different conditions; of these, high temperature and intense stimulation shorten the time, and fatigue or cold lengthen it.

Special Reflex Centres.

Many of the groups of nerve-cells in the cord are employed in executing familiar acts essential to the animal economy independent of the will. Many of these acts are very complex, and require the co-ordinated action of certain sets of muscles. Such groups of nerve-cells have been called special centres, and many of them have already been described in the preceding chapters. The more important are:

1. A centre for securing the retention of the urine by the tonic contraction of the sphincter muscle of the bladder. This group of nerve-cells is probably kept in action by impulses arriving from the bladder by the afferent nerves, passing from its walls to the spinal cord. The more distended the bladder becomes, the more powerful the stimulus sent to the cord, and therefore the more firmly the sphincter is made to contract.

2. Nearly related to the former is the centre which presides over the evacuation of the bladder. This is excited by impulses arriviny from the urethra, near the neck of the bladder. It then sets the detrusor muscle in action, while the sphincter is relaxed by voluntary inhibition.

3. The ejaculation of the semen may also be said to be accomplished by a special spinal centre, capable of controlling movements, in which involuntary muscles play an important part.

4. In parturition a number of motions are called into play (as well as the uterine contraction) which are so regularly co-ordinated, though involuntary, as to entitle us to suppose that they are arranged by a special centre in the spinal cord.

5. The act of defæcation is accomplished by means of a spinal centre also. The action of this centre might (like that presiding over the urinary bladder) be divided into two parts—retention and evacuation—in which volition and intestinal peristalsis play a very important part.

Co-ordination.

From what has been said concerning the more complex reflex actions, it is clear that the cells of the spinal cord are capable of arranging the discharge of nerve impulses, so as to bring about definite purposeful movements. This power of co-ordinating impulses, which is so striking in some reflex actions after the brain has been destroyed, is equally important in arranging efferent impulses and accomplishing ordinary voluntary movements. In fact most of the details of the mode of working of the muscles are under the control of the cells of the spinal cord.

It will help us in formulating the mechanism if we suppose the resistance in the grey part of the cord to be much greater than that in the medullated nerve channels, and that throughout it the paths are so numerous, that each individual nerve-cell might be in communication with every other nerve-cell. These paths are made passable by use; the oftener an impulse traverses a given route the more adapted such a route becomes for future traffic. Thus, by practice, we constantly freshen certain channels of intercommunication between the various cells of the cord and thus make beaten tracks, along which impulses can pass without hindrance. In a similar way certain groups of nerve-cells acquire the habit of working together and exciting complex movements which at first were impossible. The nerve-paths, along which the impulses, producing common movements, have to pass, are no doubt prepared by the long practice of our ancestors, and the power of performing these actions is transmitted to us ready for immediate application. Other paths connecting groups of cells required for the production of unusual combinations of movements have to be practised by the individual, and much

of the difficulty of learning any trade or special manual dexterity depends on the necessity of making impulses readily traverse definite directions, so as to excite certain groups of cells to act synchronously and set the required combination of muscles in accurately co-ordinated motion. Indeed, the delicacy of manipulation required by some trades cannot be attained in the lifetime of one individual; thus, it is said to require three generations to make a perfect glass-blower; the grandson having the benefit of the hereditary tendency to accomplish certain co-ordinations acquired by the life-long habit of the parents.

The importance of this technical education of the cells of the spinal cord in the execution of delicate manipulations will be felt if one attempt to imitate the movements of precision which a skilled craftsman executes without attention or voluntary effort even in the most careless exercise of his craft. The practice required for such education is experienced by anyone who attains skill in the simplest special manipulation, from writing to playing the violin.

Automatism.

Besides being excited to action by impulses coming from the brain —*volition*—and from the surface—*reflexion*—the groups of cells in the spinal cord may act without any obvious incoming impulse; that is to say, some of the cells appear to be capable of independent activity. Such groups of nerve-cells are commonly called *automatic centres;* the more important of those found in mammalia may be classified as follows:

1. Vaso-motor centres: Though the central point controlling the contraction of the blood vessels is situated in the medulla, there is no doubt that even in man, centres are distributed throughout the grey matter of the spinal marrow, which are capable of keeping up the arterial tone in the regions over which they preside. As evidence of this may be mentioned the fact that the dilatation of the arteries, which follows the severance of the lumbar part of the cord from the medulla, only lasts a few days, after which the vessels again contract in a distinctly tonic manner. The arterial tonus only disappears completely and permanently when the spinal cord is destroyed. Thus, it would appear—although habitually all the vessels of the body are regulated by a centre in the medulla, nearly related to the cardiac centre—that every vascular region has a nervous mechanism of its own in the cord, which suffices to keep up the tonic contraction of the muscular coat of its vessels.

2. Sweating centres: Though closely related to the preceding, the centres which preside over the secretion of sweat in the lower part of the body and hinder extremities must, for many reasons which cannot now be mentioned, be regarded as separate centres.

3. Some smooth muscle-fibres appear to be influenced by centres in the cord. In the lower part of the cervical cord is a group of nerve-cells which keep the sphincter muscle of the iris in check; narrowing of the pupil has been described as following injury of this region.

4. The grey matter of the cord is also said to keep the skeletal muscles in a state of slight tonic contraction; elongation of the muscles is said to follow section of the anterior roots. When this muscular tone is absent the phenomenon known as "tendon reflex" is wanting, as the tap on the tendon ceases to excite the toneless muscle.

5. So-called trophic centres are also said to exist in the spinal cord. The best evidence in this matter is derived from the skeletal muscles. If the motor nerves or roots be cut, or the anterior grey motor columns injured, the paralysed muscles soon undergo fatty degeneration, which does not depend on mere inactivity, for it does not follow cerebral paralysis, in which the integrity of the muscle can be preserved by suitable electric stimulation. Similar trophic agencies probably influence the other tissues. Thus many affections of the skin, herpes, &c., are attributed to nervous lesions.

On account of the elaborate and purposeful reflex movements performed by decapitated frogs or eels, it has been suggested that in the lower vertebrates the spinal cord is capable of sensation and volition —mental activity—but to follow this assumption, we should have to modify our ideas of volition and sensation, for which consciousness is commonly taken to be a necessary factor. It is, however, important to note that the lower we go in the scale of vertebrate animals the less powerful are the mental faculties, and the more important are the functions presided over by the spinal marrow.

CHAPTER XXXV.

THE MEDULLA OBLONGATA.

The direct continuation of the spinal cord is called the *medulla oblongata*. It consists of representatives of the various parts of the cord with some additional grey matter. The relationship of the different parts of the medulla to those of the spinal cord may be best understood by supposing the posterior median fissure and underlying nerve substance at its upper limit to be split vertically down to the central canal, and the lateral masses separated, so that the grey part becomes spread out on the posterior surface, and there forms the floor of the fourth ventricle. The *grey matter* of the medulla oblongata consists of two sets of nuclei ; one being the continuation of the grey columns of the spinal marrow, and the other made up of certain additional grey nodules embedded here and there among the white strands.

The anterior motor grey columns, which are cut off from the central grey substance by the passage of the pyramidal tract to the opposite side, are continued along the floor of the fourth ventricle near the median line. The posterior grey columns are continued upwards to form the *nucleus of Rolando*, and are spread out on the lateral part of the floor of the ventricle. Important nuclei of grey matter lie in the olivary bodies, and numerous collections of cells forming the nuclei from which arise the chief cranial nerves. For an adequate description of these groups of nerve-cells and their connections, works on anatomy must be consulted.

The various *white columns* of the spinal cord are so distributed in the medulla that their course gives some indication of the channels by which impulses are carried through it.

In ascending to the medulla the *posterior white* columns become differentiated into three. (1.) Goll's column is more distinctively marked off, and enlarges to form the *funiculus gracilis* containing the clavate nucleus, the funiculus gracilis tapers away to nothing above.

2.) Burdach's column widens in a wedge-like fashion, and is called *funiculus cuneatus*, which contains the cuneate nucleus. It passes on to help to form the inferior peduncle of the cerebellum. (3.) By the projection of the enlarged posterior grey column, *Tubercle of Rolando*, a prominence is produced called the *funiculus of Rolando*. This also helps to form the inferior peduncle of the cerebellum.

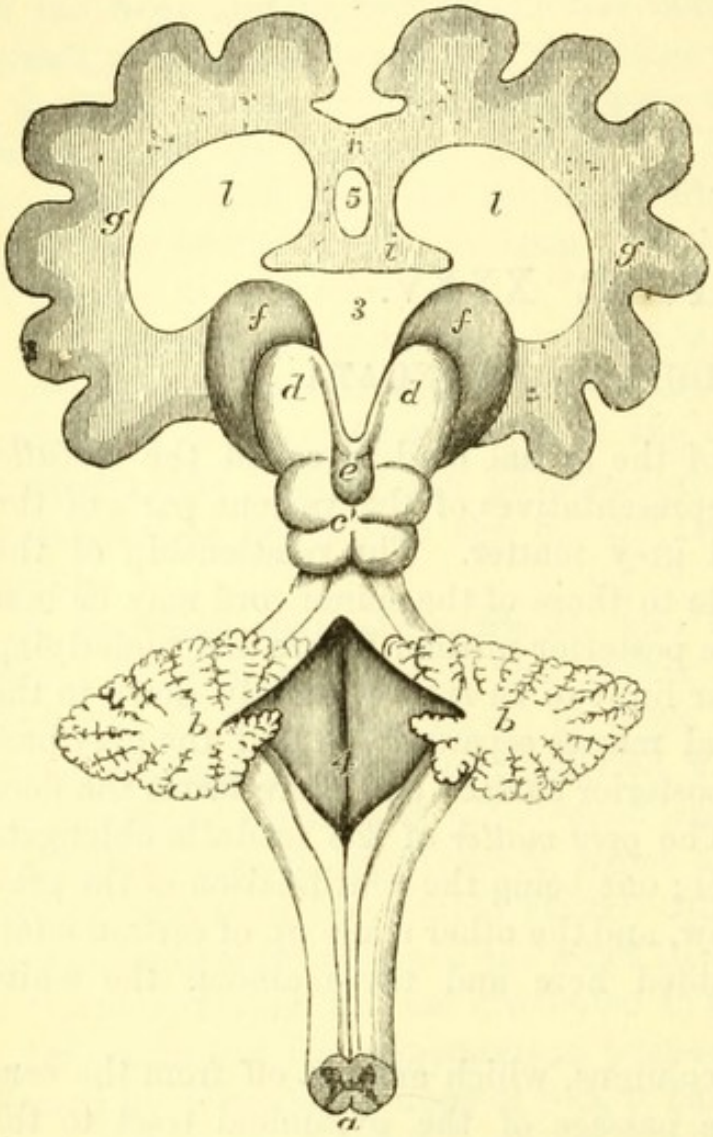


Fig. 250.—Diagram of Brain and Medulla Oblongata. (Cleland.)

a, Spinal cord; *b*, *b*, Cerebellum divided, and above it, the valve of Vieussens partially divided; *c*, Corpora quadrigemina; *d*, *d*, Optic thalami; *e*, pineal body; *f*, *f*, Corpora striata; *g*, *g*, Cerebral hemispheres in section; *h*, Corpus callosum; *i*, Fornix; *l*, *l*, Lateral ventricles; 3. Third ventricle; 4, Fourth ventricle; 5, Fifth ventricle, bounded on each side by septum lucidum.

The greater part of the *lateral white columns* of the spinal cord pass at the *decussation of the pyramids*, to the opposite side to form the pyramidal prominence on the front of the medulla, and are thence continued upward directly to the motor areas of the cortex. The *direct cerebellar tract* which forms the superficial part of the lateral column joins the cuneate and Rolando's bands to form the inferior cerebellar peduncle.

The majority of the fibres of the *anterior grey columns* pass into the medulla beneath the pyramids by which they are quite concealed. They can be traced some distance through the *pons Varolii*. The fibres of the *direct pyramidal* tracts join the pyramid of their *own side*.

It must be remembered that the medulla is the only route between the spinal cord and the upper nerve centres.

Through it all the afferent and efferent channels must pass, as they do through the spinal cord. From it, and the prolongation of its grey nuclei in the pons Varolii, several cranial nerves take origin. Thus the medulla is to the cranial nerves (from the fifth to the ninth) as the spinal cord is to the spinal nerves, but their mode of distribution is different.

The Medulla Oblongata as a Central Organ.

A number of groups of ganglion cells with special duties are located in the medulla. Those acts which are most important for the execu-

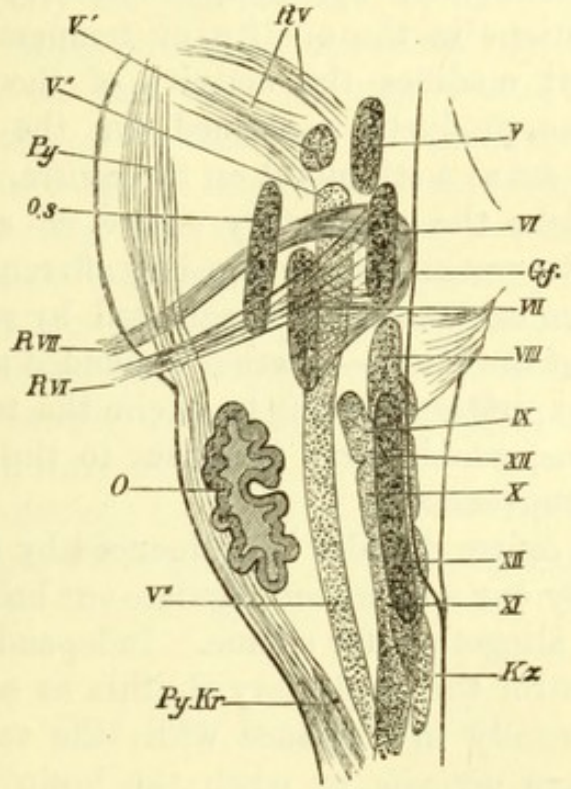


Fig. 251.—Diagram showing the position of the nuclei of the cranial nerves in the medulla oblongata, &c., as if seen in antero-posterior section, looking from the median line towards the right side. The nuclei near the median line are more darkly shaded.

Py, Pyramidal tracts; *PyKr*, Pyramidal decussation; *O*, Olivary body; *Os*, Superior olivary body; *V*, Motor; *V'*, Middle sensory; and *V''*, Lower sensory nuclei of fifth nerve; *R* V, Roots of fifth nerve; VI, Nucleus of sixth nerve *R* VI, Root of sixth nerve; VII, Nucleus; *Gf*, Knee; and *R* VII, Root of portio dura of seventh nerve; VIII, Auditory; IX, Glosso-pharyngeal; X, Vagus; XI, Accessorius; and XII, Hypoglossal nuclei; *Kz*, Clavate nuclei.

tion of the vegetative functions, are arranged and governed by the nerve-cells of the medulla. Some of these centres are called automatic, though they are variously affected by many impulses arriving from distant points, while others are purely reflex in their action.

The former are the more essential, and will therefore be first considered.

Respiratory Centre.

The centre which regulates the respiratory movements is situated in the floor of the fourth ventricle, at the upper and back part of the medulla. Flourens long since showed that injury of this spot—the *vital point*—was followed by almost instant cessation of respiration.

This is a good example of a so-called automatic centre; that is to say, the blood flowing through the medulla and nourishing the cells suffices to supply them with the energy necessary for their activity. Even slight variations in the quality or temperature of the blood reaching this part modifies the activity of the cells. The less oxygen and waste products contained in the blood, the more powerfully does it act as a stimulant on the centre.

Although we take the respiratory centre as an example of an automatic centre, its working is arranged by afferent impulses, so that the normal rhythm of breathing is regulated by reflex action. The mechanical state of the lungs—whether distended as in inspiration or contracted as in expiration—seems to excite the terminals of certain fibres of the vagus, which carry impulses to the centre, and thus excite or restrain movements.

This automatic centre can also be influenced by the higher centres of the brain, for by our will we can regulate our breathing movements or stop breathing altogether for a time. Independent of volition the higher centres control the respiratory rhythm as seen in sleep, when their action is partially in abeyance while the vagi are active, and respiration becomes *periodic*, or when the brain functions are impaired and respiration becomes *intermittent* (Cheyne-Stokes respiration). Further, the action of the respiratory centre can be altered by impulses arriving from the surface, as may be seen by the gasping inspirations which involuntarily follow the sudden application of cold.

Again, the activity of the centre may be altered by stimulations of certain parts of the air-passages; so much so, that convulsive actions of the respiratory muscles are brought about, which induced some to speak of a *sneezing centre* and a *coughing centre* in the medulla. But sneezing and coughing may be equally well explained as a peculiar form of activity of the respiratory centre, or a reflex alteration in the respiratory rhythm, caused by irritation of the nasal or laryngeal mucous membranes.

Though the action of the respiratory centre can be modified by (1) the will and (2) various peripheral stimulations, and is habitually regulated from the periphery through (3) the vagi by the state of the lungs, the *condition of the blood* supplied to the centre may be such that these remoter influences are quite powerless. This uncontrollable condition of the centre is established when the blood flowing through it is abnormally venous and the cells become over-stimulated. We know how short a time we can hold our breath by voluntary checking of the centre, and most people have had occasion to observe the inordinate and painful efforts of a person whose respiration is interfered with by disease. When the dyspnœa becomes intense, nearly all the muscles in the body are called into action. Thus, in quiet breathing comparatively few nerve-cells in the medulla carry on the work of respiration, but under certain emergencies they can call to their aid the entire motor areas of the grey substance of the spinal cord, and thus give rise to a general effort. Hence we often hear of a *convulsive centre* in the medulla being placed in close relation to the respiratory centre. In some cases, irritation of the air passages or imperfect oxidation of the blood, the convulsive centre comes under the command of the cells of the respiratory centre, which can then excite coughing, sneezing, or convulsive inspiratory effort.

As already mentioned, the convulsions of asphyxia may be explained by the impure blood acting as a stimulus on the cells of the cord itself.

The Vaso-motor Centre.

It has already been stated that groups of cells exist in the grey part of the spinal cord, which, according to the class of animal, have more or less direct influence upon the muscles in the coats of the vessels. Thus in a frog, whose brain and medulla have been destroyed, in some hours the vessels of the web regain a considerable degree of constriction, which is again lost if the cord be destroyed. In the dog the vessels of the hinder limb recover their tone more or less perfectly in a few days after the spinal cord has been cut in the dorsal region, although just after the section they are widely dilated from the paralysis of their muscular coats. In a few days the cells of the cord can learn to accomplish, of their own accord, work which they have been in the habit of doing, only under the direction of the higher centre. From this we conclude that though the cord contains local vaso-motor centres distributed throughout its grey matter

these are normally under the control of the vaso-motor centre in the medulla, and this centre is really the chief station from which impulses destined to affect all the blood-vessels must emanate.

This arrangement is quite comparable with that by which the ordinary muscles are made to contract. When the will causes a muscular contraction, the impulse starting from the cerebral cortex does not travel directly to the muscle, but it passes from the brain to certain cells in the cord and thence to the muscles. In fact, to these spinal agents the ultimate arrangement and co-ordination of the act is confided. So, also, the chief vaso-motor centre in the medulla executes its function through the medium of numerous under-centres placed at various stations along the cord.

The vaso-motor centres—like nearly all other controlling groups of ganglion cells—may be considered as composed of two parts antagonistic one to the other, viz., a *constricting* and *dilating* centre, the impulses from which travel by separate nerve channels. The constricting impulses are mainly distributed by the sympathetic nerve, while the dilating impulses accompany those which are employed in calling forth the ordinary function of the part in question.

From what has been said as to the wide distribution of centres influencing the blood-vessels, an attempt to localise exactly the position of the medullary vaso-motor cells is not satisfactory. In lower animals—frogs—the cells are evenly diffused throughout the medulla and cord. In man the localisation is difficult to demonstrate, though we have reasons for thinking it much more definitely circumscribed. In the rabbit it has been localised to the floor of the fourth ventricle in the immediate neighbourhood of the respiratory and cardiac centres. From this the nerves pass by the cord to the spinal roots, by which they reach the sympathetic.

The vaso-motor centre exerts a tonic or continuing action on the vessels, holding them in a state of partial constriction or *tone*. In this it may be said to have an automatic action. Although this tonic state of activity of the centre may be called automatic, it is really under the control of many reflex influences, which constantly vary the general tone, or effect local changes in the degree of constriction of this or that vascular area. Among the most striking afferent regulating impulses are those arriving from the heart, the digestive organs and the skin. In some animals, a special nerve—the depressor—has been discovered, which, passing from the heart to the medulla, keeps the vaso-motor centre informed as to the degree of tension, &c., of the heart cavities. When the heart becomes overfull, impulses pass from it, and check the tonic power of the centre,

so as to reduce the arterial pressure against which the ventricle has to act. Electric stimulation of this nerve causes a remarkable fall in the general blood pressure. The vaso-motor centres regulate the distribution of blood to the viscera and skin, according to the condition of activity of these parts as described in another chapter (XXXI.).

The Cardiac Centre.

Although the heart beats periodically when cut off from the nervous centres, its normal rhythm is under the control of a group of nerve-cells in the medulla, from which some fibres of the vagus carry special regulating impulses to the heart. The action of this centre is habitually that of a restraining agent lessening the rate of the heart's contractions, and is hence called a tonic inhibitory centre. The activity of the centre is influenced by the condition of many distant parts, such as the cortex of the brain, the abdominal viscera, &c., which exert a kind of reflex action on the heart through the centre. The degree of inhibitory power, as well as the share taken in the action of the centre by automatism and reflection, differs in different animals. A centre (*accelerator*) antagonistic to the latter also exists in the medulla. It is weaker in action than the inhibitory centre, and is not tonic.

In the medulla there also exist many other centres connected with the organic functions. Among these the centres for swallowing and vomiting may be mentioned. For further details on this subject, the reader may consult the chapter on Digestion.

CHAPTER XXXVI.

THE BRAIN.

As we pass upwards in attempting to trace the conducting channels of the medulla, we come to the more elaborate system of nervous textures which, together, are called the brain. This is anatomically the most highly developed, and physiologically the most intricate, part of the central nervous organs. Besides the nerve-cells and various kinds of conducting channels with which we have already become familiar in the cord, &c., there are in the brain a vast number of smaller elements which do not possess the distinctive characteristics of nerve-cells. These granular bodies are tightly packed together in many parts of the centres, and must have some important function.

To form a general idea of the plan of construction of the brain, it is well to follow its development in the earlier stages of the embryo, from the time when it forms an irregular and thickened part of the tube of tissue, from which is developed the cerebro-spinal axis. From this it will be seen that the brain is but a modified part of the primitive nervous tube, in which swellings may be observed at an early period of embryonic life. These swellings are called the fore-brain, mid-brain, and hind-brain, and in the future development of the parts give rise to (1) the hemispheres and basal ganglia; (2) the corpora quadrigemina, pons, and cerebellum; and (3) the medulla oblongata. The great mass of the brain—the hemispheres—is formed by an excessive development of bud-like processes which grow out from the sides of the fore-brain at an early period, and become elaborately folded, so that in the adult it is difficult to trace the relationship to the original form. For further details of the development of the brain, *vide* chapter on that subject.

The cells of the brain are, like those of the cord, grouped together in the complex grey substance, while the white part is made up of conducting fibres. The grey substance is distributed in four distinct regions. (1.) Of these one can be traced along the floor of

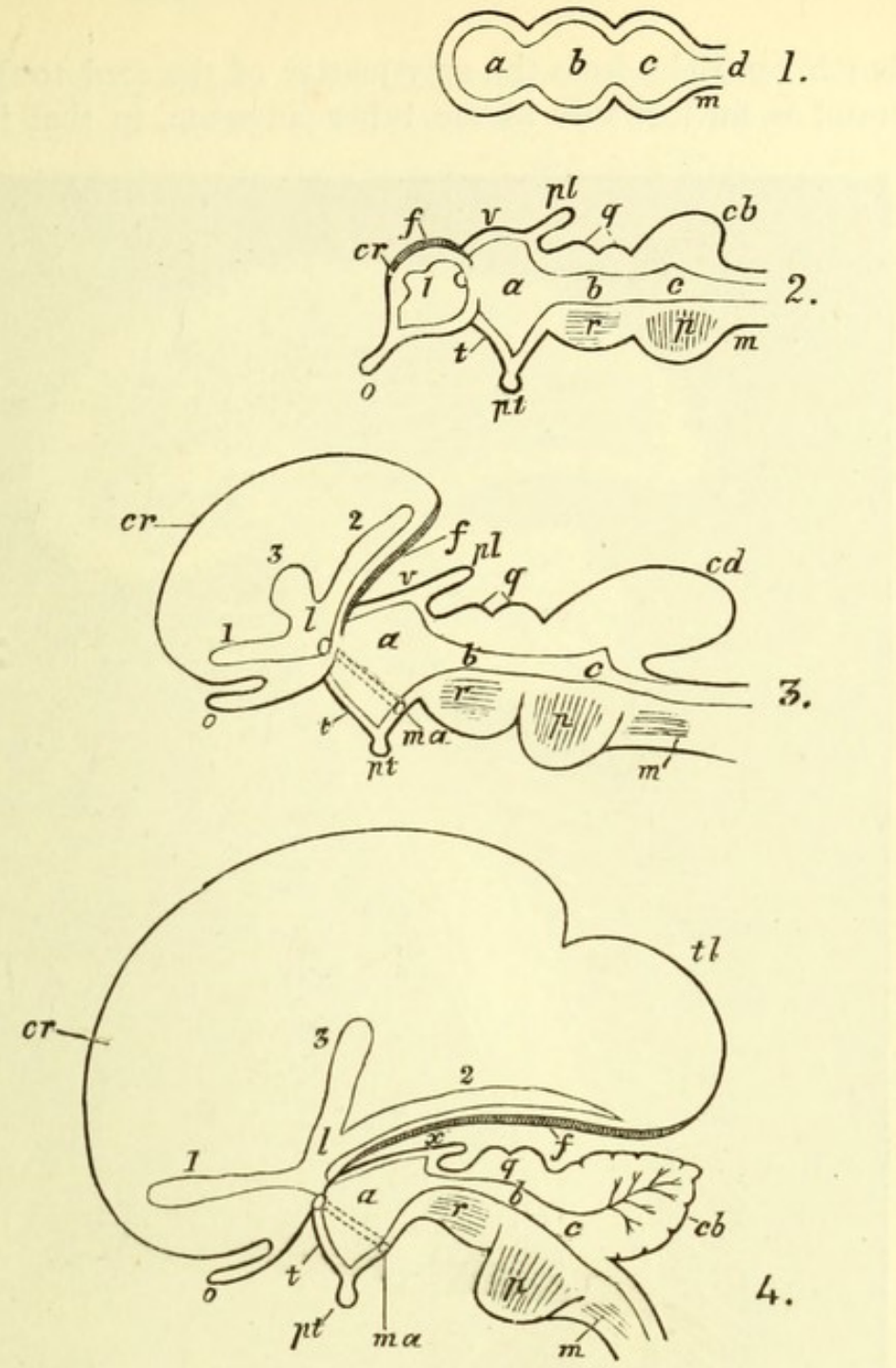


Fig. 252.—Diagram illustrating the progressive changes in the development of the brain.

1. Shows the first step; the formation of three vesicles.
2. Shows the budding forwards of the hemispheres (*cr*), upwards of the pineal gland (*pl*), and downwards of the pituitary body (*pt*) from the fore-brain (*a*), and the thickening of the mid (*b*), and hind-brain (*c*).
3. Shows the backward turn of the hemispheres and their cavity (lateral ventricle) (*l*). The development of the corpora quadrigemina (*q*) and crura (*r*) from the mid-brain (*b*) and the cerebellum (*cd*) and pons (*p*) from the hind-brain; their cavities being narrowed into the *iter a tertio ad quartum ventriculum*.
4. The hemispheres now extend backwards and form the temporal lobe (*tl*), which afterwards grows downwards and forwards. The fornix (*f*) approaches its final position. The space (*x*) between the fornix and velum is closing, so that the outside of the brain (morphologically) becomes practically its very centre.

Explanation of letters.—*a*, Fore-brain; *b*, Mid-brain; *c*, Hind-brain; *cb*, Cerebellum; *cr*, Cerebrum; *d*, Cavity of medulla; *f*, Fornix; *l*, Lateral ventricle; *m*, Medulla oblongata; *ma*, Corpora mammillaria; *o*, Olfactory lobe; *p*, Pons Varolii; *pl*, Pineal gland; *pt*, Pituitary body; *q*, Corpora quadrigemina; *r*, Crura cerebri; *t*, Lamina terminalis; *tl*, Temporal lobe of cerebrum; *x*, Space enclosed by the extension backwards of the cerebrum.

the fourth ventricle, from the grey matter of the cord to the base of the brain, as far forwards as the tuber cinereum, so that it may be

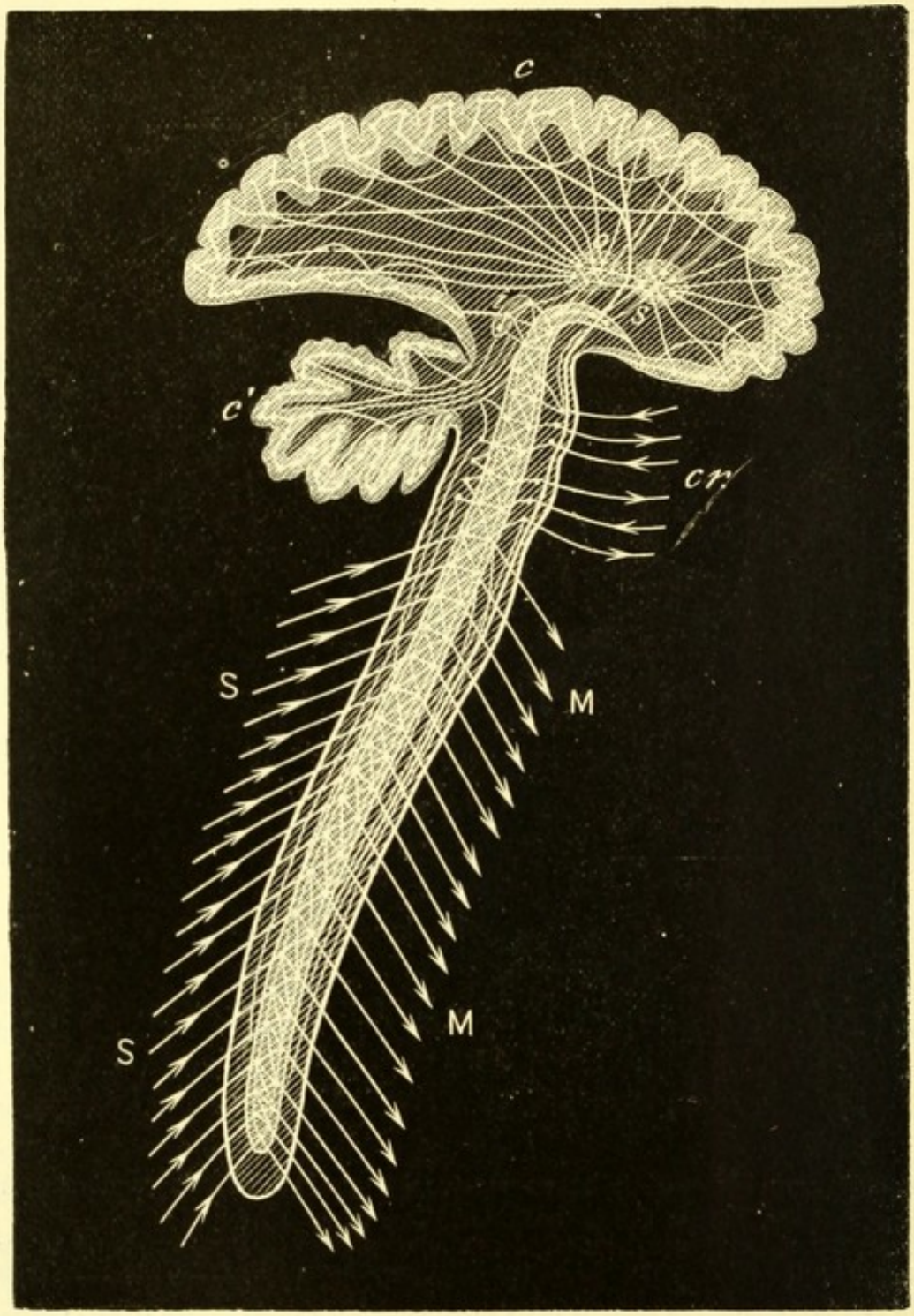


Fig. 253.—Diagram of some of the paths taken by nerve impulses in the brain and spinal cord.

c. Grey substance of cerebral cortex. *c'*. Grey substance of cerebellum.
cr. Cranial nerves, some afferent and some efferent.
M. Motor (efferent) spinal nerves. S. Sensory (afferent) spinal nerves.

considered representative of the grey matter forming the inner lining of the primitive nervous tube. (2.) The ganglia of the brain are isolated masses of grey substance within the brain, known as

the corpora quadrigemina, optic thalami, corpora striata, &c. (3.) The grey substance of the cerebellum and of the corpora quadrigemina is derived from the upper part of the mid-brain. (4.) The cortex of the hemispheres of the brain is the most extensive grey district, and must be regarded as distinct from the preceding.

Connecting the various parts of these grey regions are sets of fibres, which may be classified as follows :—

1. Those which act as channels of intercommunication for the different parts of the same region. These may be divided into *unilateral*, which connect together the cells of a single hemisphere, and *bilateral*, or commissural fibres, which unite the corresponding masses of grey matter on both sides of the brain.

2. Those which connect the different regions one with another. Under this head fall (1) those fibres which pass between the cortex and the basal ganglia, or anterior grey column of the spinal cord ; (2) those running from the cortex or the spinal cord to the cerebellum ; and (3) those connecting the above with the spinal grey matter.

The Mesencephalon and Cerebellum.

In examining the functions of the brain, we may consider the various parts in the order they are found in proceeding from the medulla towards the cerebral hemispheres. Between the medulla oblongata and the hemispheres, we come to the pons Varolii and cerebellum, the crura cerebri, and corpora quadrigemina, which being developed from the mid-brain, may be called the mesencephalon. The duties of these parts of these nervous centres can be investigated by observing the actions of lower animals in which the hemispheres have been removed or the parts directly stimulated, and by noting the symptoms produced in man by lesions of this part of the brain. The former method gives the most definite results, and therefore deserves most attention.

In all these parts there are innumerable fibres capable of conducting impulses in many directions, and numerous masses of ganglionic cells distributed throughout the white substance. In the cerebellum a remarkable layer of large branching cells divides the central from the cortical tissue.

When the cerebral hemispheres have been removed from a frog, the animal retains the power of carrying out co-ordinated motions of much greater complexity than those performed by the spinal cord alone. But this power is not exercised spontaneously. That is to

say, the animal can balance itself accurately, jump, swim, swallow, &c., but it only attempts these acts when excited to do so by stimulations from its outer surroundings. Thus on a flat surface

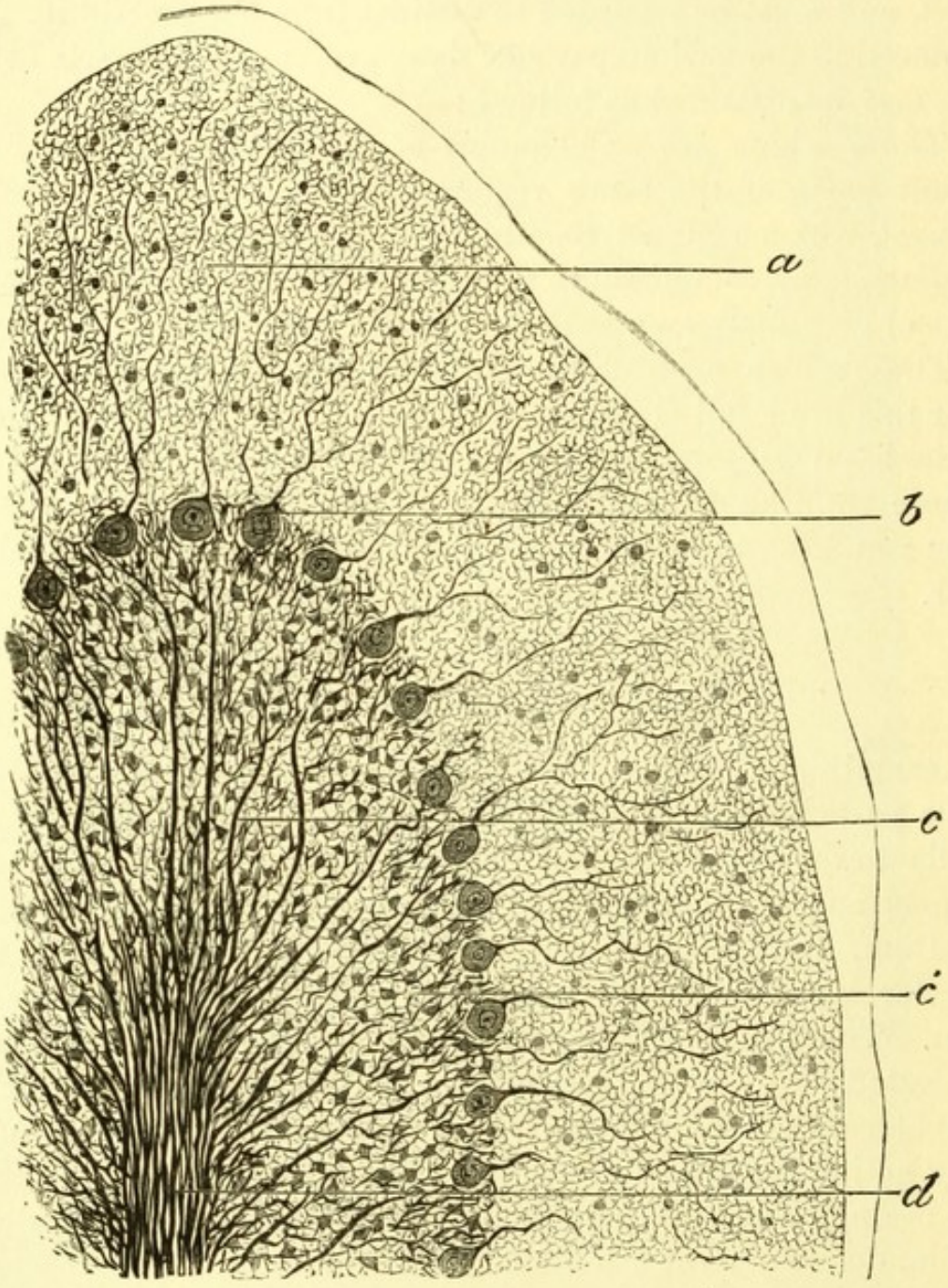


Fig. 254.—Section through a part of the cerebellum.

a, Molecular layer into which pass the branches of Purkinje's cells, *b*; *d*, Medullary centre from which medullated fibres pass through the granular layer of nervous and neuroglia cells to reach the cells of Purkinje.

it sits upright, but does not stir from the spot where it has been placed; if the surface upon which it sits be inclined, so that its head is too low, it turns round to regain its ordinary position. If the surface be further inclined, it at first crouches so as not to slip off,

and then crawls upwards to find an even resting place. Plunged into water, it swims perfectly, but on arriving in a shallow part, it either rests quietly with its nose out of the water, and its toes touching the ground, or crawls out to sit on the water's edge, where it can find its balance. When touched on the leg, it jumps away from the stimulus, and in so doing avoids any obvious dark obstacle. It swallows if a substance be put in its mouth, but does not attempt to eat even if surrounded with food. In short, all movements, even the most complex, may be brought about by adequate stimulation—*spontaneity* only is wanting. The pupil responds by reflex contraction, when the retina is exposed to light ; the eyes are closed if the light be intense ; and the head may follow the motions of a flame moved from side to side. A sudden or loud noise causes it to move. From the foregoing facts, and the power such a frog has of avoiding a dark object, we may conclude that the impulses arriving from the special sense organs are all duly received, and excite more or less elaborate response, but that the *consciousness* of the arrival of these impulses no longer exists.

The removal of the hemispheres of birds and rabbits leaves the animal in a somewhat similar condition ; but the response to the special sense impulses is not so definite or well marked since the animal flies or runs against even the most obvious obstacles.

We may conclude, then, that the medulla controls the co-ordinated movements absolutely necessary for the vegetative functions, and that the mid-brain (including the cerebellum of birds and mammals) controls the complex associations of co-ordinated movements necessary for the perfect performance of such acts as standing and walking.

The enormous number of muscles simultaneously used in some of our commonest daily actions, concerning which we have but little thought, and take no voluntary trouble, shows the great importance of this part of the brain. If we take a simple example, that of standing in the upright position (*equilibration*) (see page 410) we find that a great number of muscles have to act together with the most exact nicety to accomplish what, even in man, is an unconscious, if not quite involuntary, action. In the frog, as has been seen, equilibration is performed by reflex action alone. In man, the nervous mechanisms are probably more complicated by his erect attitude and the addition of the cerebellum, &c., but they are nevertheless comparable with those of the frog. It may therefore be instructive to examine the details of the mechanisms in a frog deprived of its cerebral hemispheres.

The *optic lobes* of the frog's brain (which correspond to the corpora

quadrigemina, and also take the place of the cerebellum of the higher animals) form the great centres of equilibration, locomotion, &c. If these lobes be destroyed, the animal can no longer sit upright, jump or swim. The first point to determine is, whence do the impulses arrive which bring about these complex co-ordinations. The first set is that coming from the tactile sense of the skin of those parts touching the ground. A second set arrives from the acting muscles indicating to the centres the amount of work done (*muscular sense*). A third set comes from the eyes, by which the position of the surrounding objects is gauged. Finally comes the fourth set from the semicircular canals of the internal ear, which communicate to the equilibrating centres the position of the head.

By depriving a frog of these several portals by which incoming stimuli direct the balancing centres, it can be rendered incapable of any of the acts requiring equilibration, even when the regulating centres are intact. In our own bodies we can convince ourselves of the importance of these afferent regulating impulses arriving from the eye, ear, skin, and muscles. When the eyes are shut and heels together we cannot stand as steadily as when we keep our eyes fixed on something ; even with care not to move, we sway slowly to and fro. If having bent our head to the handle of a walking stick, the end of which is fixed on the ground, we run three or four times around this axis so as to disturb the fluid in the semicircular canals, and then attempt to walk straight, we find how helpless our volition becomes when deprived of the aid naturally coming from special mechanisms in the internal ear.

When the feet are "asleep" or benumbed, standing or walking can only be performed in a most awkward manner, showing the necessity of tactile sensation for perfect equilibration. In a disease known as *locomotor ataxy* the muscular sense is lost, and the power of standing or walking correspondingly impaired.

Crura Cerebri.

Passing above the *Pons Varolii*, we come to an isthmus, composed of two thick strands of nerve substance connecting the pons Varolii with the cerebral hemispheres. These are called the crura cerebri. They diverge slightly in their upward course towards the hemispheres, and lie just below the corpora quadrigemina, already referred to Minute examination of these crura brings to light an anatomical difference which corresponds with a physiological separation between

the paths taken by the sensory and motor impulses in each crus. The lower and more anterior part, which can be seen on the base of the brain, is called the base or *crusta*. This is made up of efferent nerve channels only. The posterior or upper part, which lies next to, and is connected with the corpora quadrigemina, is called the *tegmentum*, and is composed of afferent fibres. Anatomically the separation between the two is indicated by some scattered nerve-cells (*locus niger*). The base, or crusta, which is the great bond of union between the spinal cord and the cerebral motor centres, passes into the corpus striatum; and the tegmentum, or great sensory tract, is directly connected with the optic thalamus.

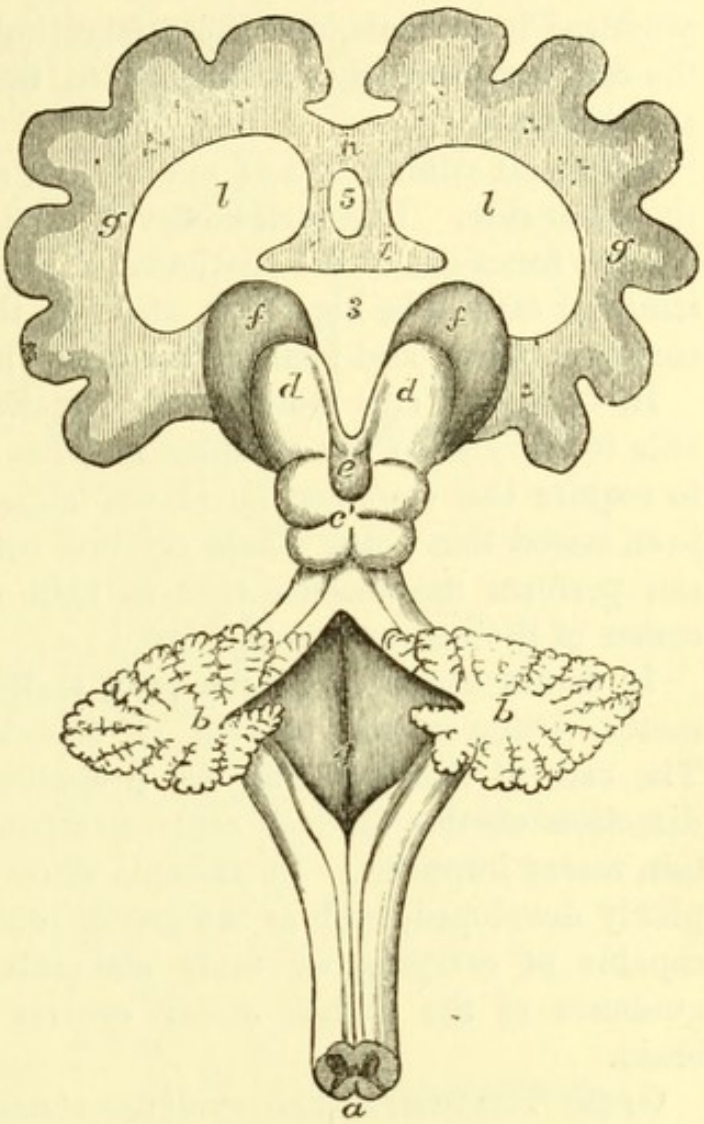


Fig. 255.—Diagram of Brain and Medulla Oblongata. (Cleland.)

a, Spinal cord; *b*, *b*, Cerebellum divided, and above it, the valve of Vieussens partially divided; *c*, Corpora quadrigemina; *d*, *d*, Optic thalami; *e*, pineal body; *f*, *f*, Corpora striata; *g*, *g*, Cerebral hemispheres in section; *h*, Corpus callosum; *i*, Fornix; *l*, *l*, Lateral ventricles; 3, Third ventricle; 4, Fourth ventricle; 5, Fift ventricle, bounded on each side by septum lucidum.

Basal Ganglia.

On the floor of the lateral ventricles are the *corpora striata* and *optic thalami*, which together are spoken of as the basal ganglia. The exact relationship borne by their functions to those of the mesencephalon and cerebral cortex is not perfectly understood. The following are some of the more important points in the evidence on the subject :—

Corpora Striata.—The motor tracts, coming from below, lie in the lower part of the crus cerebri, and thence one on each side passes

into the corresponding corpus striatum. Anatomically this part may be regarded as the ganglion of the motor tract.

Destructive lesion of one corpus striatum is followed by loss of motion of the other side. This is equally true of lesions artificially produced in animals, and those resulting from disease in man. When the crura on both sides are destroyed the animal remains motionless and prostrate.

Electrical stimulation of one corpus striatum causes movement of the other side. This fact, however, does not teach us much concerning the functions of the particular cells of its grey matter, since the stimulus cannot be kept from affecting the fibres passing through the corpus striatum and forming the direct motor tract.

In dogs, and still more in rabbits, the corpora striata seem to be able to carry out some complex motions which in man are believed to require the co-operation of the higher cerebral centres. It has been stated that a dog whose cerebral cortex is completely destroyed can perform movements that in man can only be evoked by the cortex of the hemispheres.

It would appear that the grey matter of the corpus striatum is motor, being nearly related in function to the cerebral cortex. The cells of this ganglion are probably agents working under the direction of the cortical centres, organizing and distributing certain motor impulses. In animals whose hemispheres are less complexly developed, such as the dog or rabbit, the "basal agent" seems capable of carrying on more elaborate work, independent of the guidance of the higher motor centres in the grey matter of the brain.

Optic Thalami.—The evidence concerning the function of these ganglionic masses is far from being even as satisfactory or conclusive as that relating to the corpora striata.

Anatomically their relationship is equally clear; they are the ganglia of the sensory tracts, since the tegmentum or sensory parts of the crura pass directly into them. They form the chief routes by which impulses, giving rise to different sensory impressions, arrive at the cerebral cortex. But the evidence we obtain by the physiological examination of sensory impressions is indistinct compared with the results when motor tracts are excited. In the complete absence of all motion, it is impossible to know whether an animal feels or not, as we have no other signs of the stimulus taking effect. It is difficult, as has been already seen, to stimulate any sensory tract without the impulse being reflected to its motor neighbours, so a muscular movement often results from stimulation of a group of

cells purely sensory in function, and yet is not decisive evidence of conscious sensation.

When we take into consideration the foregoing points, and the fact that it is difficult, if not impossible, to destroy a portion of brain substance without irritating it and the neighbouring structures, we cannot be surprised that experimenters have arrived at very contradictory results, both by stimulating and destroying the optic thalami. Some find that electric stimulation causes muscular movements; others find that it does not.

Some authorities state that destruction of the optic thalami interrupts only the incoming sensory impressions; others say it gives rise to motor paralysis.

Human pathology helps us but little, for it is impossible to say whether a lesion simply abo-

Fig. 256.—Section through the cortex of temporal lobe of monkey showing the series of layers of nervous cells with different chara cters.

lishes the function or acts as an irritant, or produces both these effects. Local lesions of the optic thalami have been met with, in some of which sensory, in others both sensory and motor defects have been observed in the patients.

We must remember that the occurrence of motion as the result of stimulation, or the absence of muscular power as the result of destruction of the optic thalami must not be accepted as good evidence of the motor function of the nerve-cells of this part, because these results may depend on the indirect influence of the sensory impulses coming from these cells.

Cerebral Hemispheres.

It is now universally regarded as a recognised fact that the hemispheres of the brain are the seat of the mental faculties—percep-

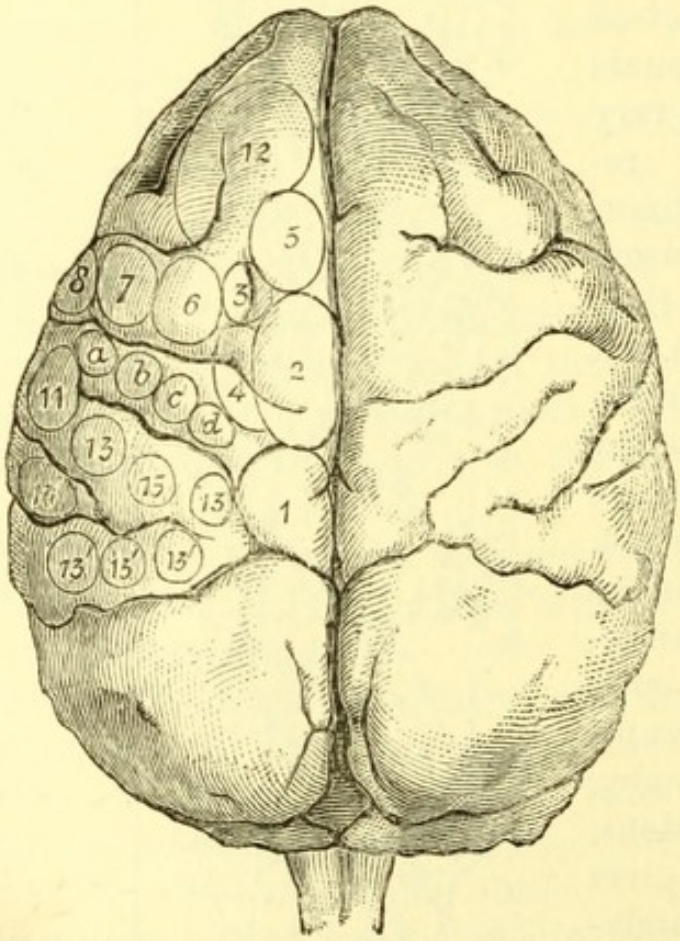


Fig. 257.—Upper surface of the hemispheres of monkey, showing details of motor areas. References as in next figure. (Ferrier.)

tion, memory, thought, and volition. The cerebral cortex is the part of the nervous system in which the subjective perception of the various sensory impulses takes place, and in which impulses are

converted into impressions or mental operations. It is in the cortical nerve-cells that the so-called voluntary impulses, causing movement of the skeletal muscles, have their origin. It is thus a sensory and a motor organ. But it has a far wider range of function than is ex-

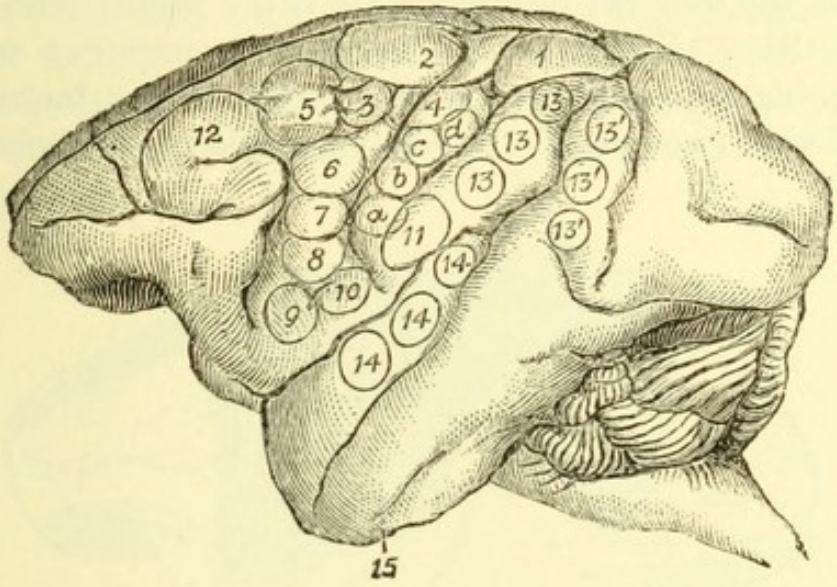


Fig. 258.—Left hemisphere of monkey, showing details of motor areas indicated by the movements following stimulation of,—

1. Superior parietal lobule; exciting advance of the hind limb.
2. Top of ascending frontal and parietal convolutions; flexion and outward rotation of thigh; flexion of toes.
3. On ascending frontal convolution near semi-lunar sulcus; movements of hind limb, tail and extremity of trunk.
4. On adjacent margins of ascending frontal and parietal convolution; adduction and extension of arm, pronation of hand.
5. Top of ascending frontal near superior frontal convolution; forward extension of arm.

a, *b*, *c*, *d*, On ascending parietal; movements of various muscles of the fore-arm.

6. Ascending frontal convolution; flexion of fore-arm and supination of hand which is brought towards mouth.
7. Retraction and elevation of corner of mouth.
8. Elevation of nose and lip.

9 and 10. Opening mouth and motions of tongue.

11. Retraction of angle of mouth.
12. Middle and superior frontal convolutions; movements of head and eyelids.
13. and 13′. Anterior and posterior limbs of angular gyrus; movements of eyeballs.
14. Superior tempero-sphenoidal convolution, ear pricked, and head moved.
15. Movement of lip and nostril. (Ferrier.)

pressed by saying it is both sensory and motor. Thus restricted, its function would be no higher than that of the nerve-centres in the spinal cord, &c. The cells of the cortex of the brain seem to differ from those of the lower nerve-centres, which can only receive, and at once send out corresponding impulses, in this: when an impulse arrives at certain cerebral cells, it there excites a change, which,

besides producing an immediate effect, leaves a more or less permanent impression. The impression persisting, if the cell be well supplied with chemical energy in the shape of nutriment, it may be reproduced at a subsequent period. This revival of impressions, the effects of past stimulations, or "recollection" is exclusively the property of the cerebral cortex, and to it the hemispheres owe their mental faculties. During our lifetime sensory impulses are continually streaming into the cells of the cortex of the brain from the peripheral sensory organs. Thus innumerable impressions are stored

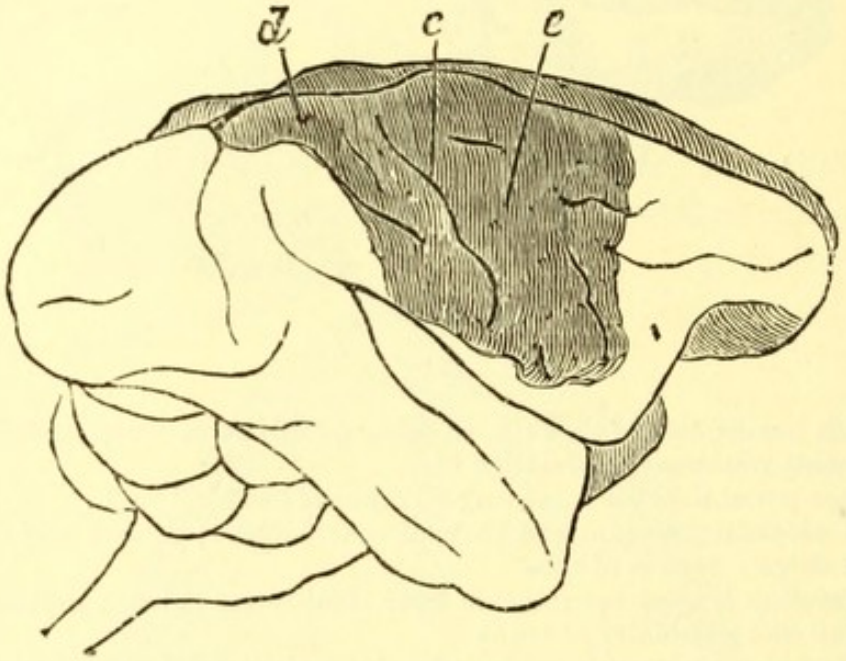


Fig. 259.—Dark shading indicates the extent of a lesion of the grey matter of the right hemisphere of a monkey followed by complete motor paralysis of the limbs of the opposite side without impairment of sensation. (Ferrier.)
c, Fissure of Rolando; *d*, Postero-parietal lobule; *e*, Ascending frontal convolution.

up in the nerve-cells. The effect of the continuing presence of these impressions in the active cells is *memory*, and by association, arrangement or analysis of these persisting impressions, the activity of the cells gives rise to thought or ideation.

In close relation and connection with these cells of the cortex, in which permanent impressions are stored and ideation is accomplished, are those other groups of cells which have been mentioned as being in direct communication with the spinal motor centres, and can by the medium of the latter execute voluntary movement.

It is a very remarkable fact, that one side of the brain is sufficient for the perfect performance of the mental faculties. Memory, consciousness, and thought can all be operative in a perfectly normal way, when one side of the brain is rendered incapable of performing its functions by disease or injury.

This is not the case as regards sensory impressions, or voluntary movement, both of which are destroyed on the side of the body opposite to that of the injured hemisphere. The difference between the mental powers and mere motor and sensory functions of the brain can be seen in those cases of paralysis known as hemiplegia. The patient is frequently fully conscious, and may possess unimpaired powers of thought and memory, yet he is unable to perceive the sensory impulses coming from one side of his body, or to send voluntary impulses to the muscles of the paralysed side.

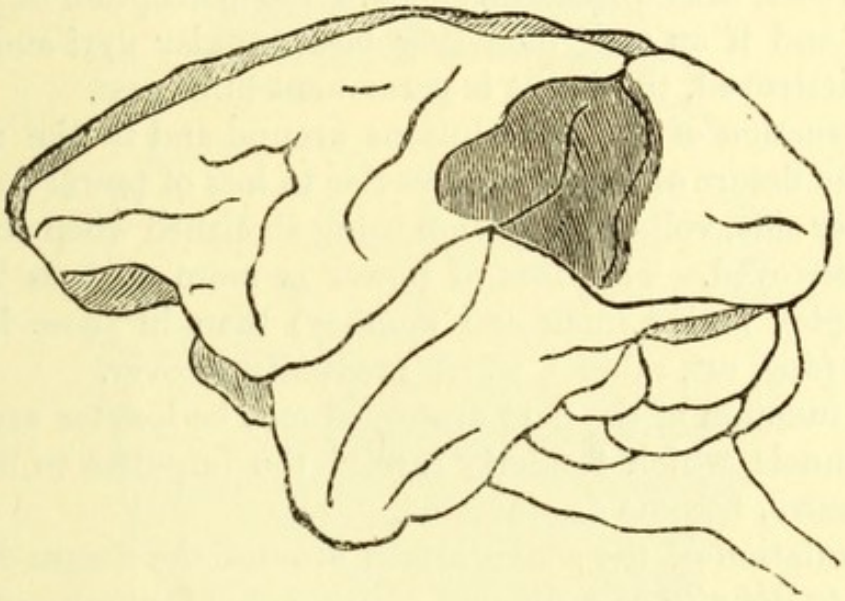


Fig. 260.—The dark shading shows the region of the angular gyrus of a monkey, injury of which is followed by transient blindness. (Ferrier.)

The cells which act as the immediate receivers of afferent, and dispensers of efferent impulses, to one or other side of the body, are then localized to one hemisphere, viz., that of the opposite side, while mental operations are diffused over the cortex of both hemispheres.

Localization of the Cerebral Functions.

Whether the entire surface of the hemispheres can be mapped out into areas, each of which is set apart for a definite immutable function, is a question surrounded with difficulty, and which, up to the present, cannot be answered with certainty. The experimental evidence hitherto brought forward on the subject seems, in some points, to be contradictory, a fact which may be explained partly by the difficulties with which such experiments are beset, and partly by different

observers being anxious to uphold with too great fervour either the localization or non-localization theory.

The evidence on this subject may be briefly summarised as follows. In favour of localization are the facts that :—

1. Lesion of a certain part of the cortex of the frontal lobe of the left hemisphere of man (posterior part of the third frontal convolution) has been so frequently followed by the loss of memory of words necessary for the faculty of speech—*aphasia*—that pathologists now call that spot the *speech-centre*.

2. Destruction of the cortical surface of the angular gyri, or of the posterior lobes, causes transitory loss of the perception of visual impressions, and if an area, including both angular gyri and posterior lobes be destroyed, the result is permanent blindness.

3. Destruction of the convolutions around and in the neighbourhood of the fissure of Rolando gives rise to loss of power in the limbs of the other side, voluntary motion being abolished when an extensive area is destroyed. This loss of power is more obvious in animals with complex brains (man and monkey) than in those less highly organized (dog, cat, rabbit), which gradually recover.

4. The function of the part destroyed may be lost for ever, and the nerve channels, which formerly carried the impulses to or from the injured centre, become degenerated.

5. Stimulation of the convolutions around the fissure of Rolando gives rise to definite co-ordinated movements of muscles of the other side. Local groups of muscle respond with striking constancy to the electric stimulation of certain definite and limited areas of the cortex. These convolutions have been mapped out into motor centres for hind limb, fore limb, face, &c. Compare Figs. 257 and 258.

From the foregoing we may safely conclude (1) that certain parts of the cortex of the hemispheres are the agents for the reception of definite sensory impressions ; (2) that others (the neighbourhood of the fissure of Rolando) are related to the discharge of voluntary motor impulses ; and (3) though we cannot say that the anterior lobes are immediately subservient to either the sensory or motor functions, a portion of one of them seems devoted to the memory of words.

As objections to the soundness of these conclusions, it has been urged :—

1. Considerable discordance still exists in the results arrived at by different experimentors.

2. The function returns after the lapse of a variable interval, particularly in unilateral destruction of the cortical centres. In some instances the loss of function only continues for a few hours

after the operation ; in others (those in which the injury is extensive and deep, or the animal belongs to a class with high mental organization) the recovery is slow and may extend over several weeks or months.

3. Certain tracts of the cortex of the hemispheres, notably the anterior and posterior lobes, may be extensively injured, by accident

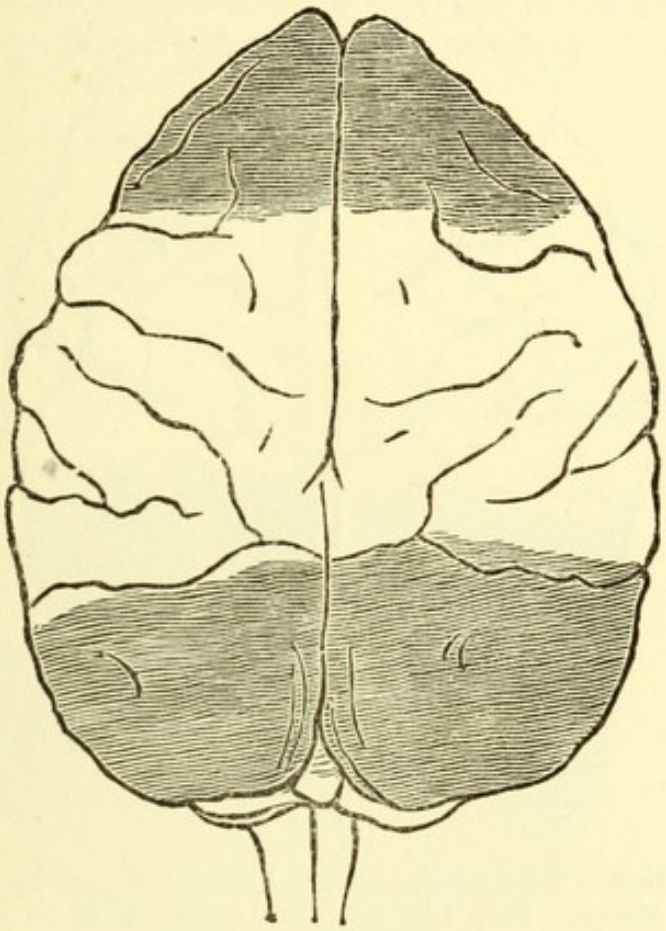


Fig. 261.—The dark shading shows areas which were destroyed in a monkey without giving rise to any functional defect that could be detected. (Ferrier.)

or experiment, without interfering with the cerebral functions in any marked or tangible way. Both men and animals have lived for years, after the loss of a considerable quantity of brain substance, without showing impairment of either mental or bodily faculties.

4. Certain areas of the brain surface may be stimulated mechanically, chemically, or electrically, without the least response being shown by the animal, to indicate either sensory or motor excitations.

In spite of this negative evidence from the facts just adduced—viz., that certain groups of muscles respond regularly to the stimulation of local areas of the brain surface, and that loss of function of some organ occurs when a given point is injured—it seems definitely fixed

that certain local parts of the brain surface are in more immediate connection with definite peripheral organs than with others, and that these local areas have been in the habit of receiving or sending out special impulses.

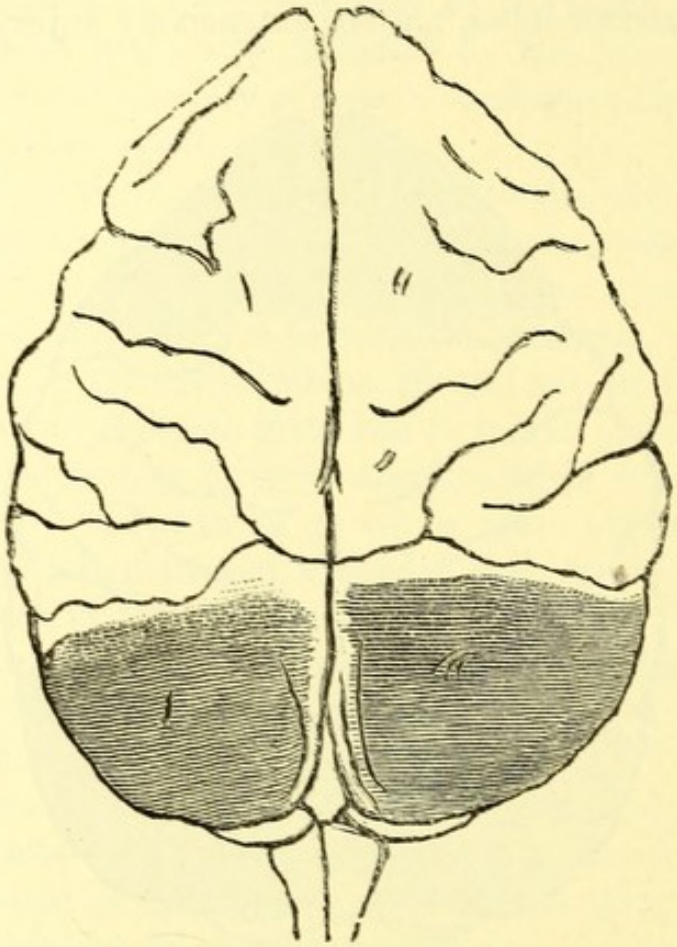


Fig. 262.—Extirpation of the posterior lobes. Lesion followed by only transient disturbance of vision. In a few hours no defect could be detected in any of the animal's functions. Some observers have found total blindness after a lesion but slightly greater than that here shown. (Ferrier.)

The evidence is strongest in support of the *motor* areas situated around the fissure of Rolondo in the central region of the hemispheres. Here (1) limited stimulus excites definite action, (2) circumscribed lesion is followed by local paralysis, and (3) after lesion a tract of degeneration unites the cortical and spinal centres engaged in the production of voluntary movement.

With regard to the sensory centres the areas are not so perfectly localized. We can hardly suppose that all the grey matter of the angular gyri and occipital lobes are devoted exclusively to the reception of visual impressions. Yet it has been stated all this region must be destroyed to annihilate the visual function.

From the fact that its stimulation causes movements of the pinna

and its destruction is said to abolish hearing, the *superior tempero-sphenoidal convolution* has been allotted the function of an auditory centre. From somewhat similar evidence, and that gained from anatomy, the *hippocampal lobule* is said to be the seat of smell.

Ordinary sensation has been localized to the inferior tempero-sphenoidal convolution and the hippocampal region owing to the anæsthesia found after destruction of these parts.

From the other facts mentioned—viz., the absence of functional disturbance after cortical lesion and the recovery of function after

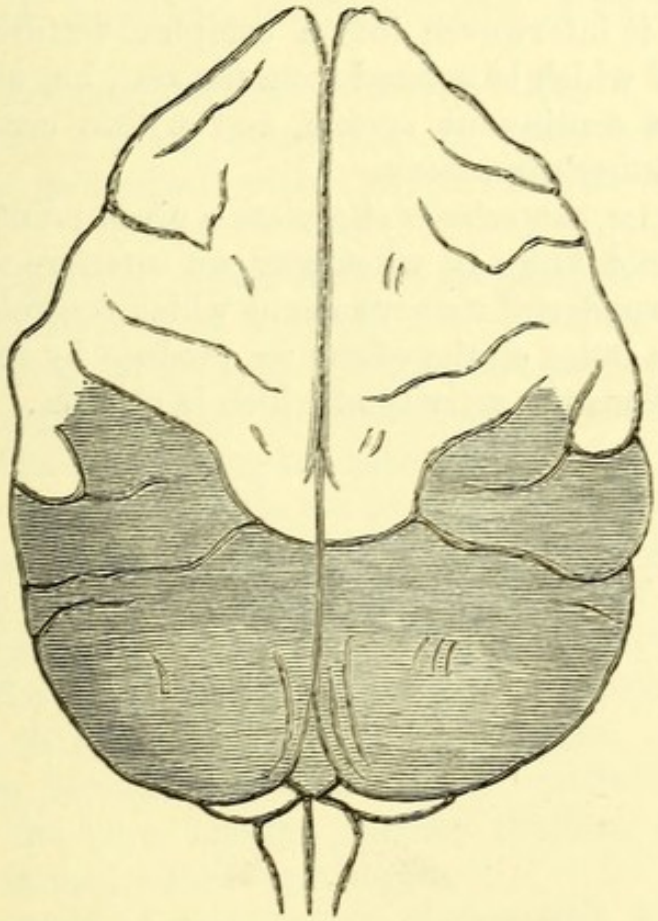


Fig. 263.—The shading shows the great extent of surface destroyed before permanent cortical blindness followed by retinal atrophy was produced: *i.e.*, all posterior lobes and angular gyri.

injury, we must conclude that there are extensive tracts containing cells to which we can assign no localized function, and that the local areas to which a function can be assigned are not the only agents which can carry on the business of receiving impulses from the periphery, and sending voluntary impulses to the muscles; but that there are many groups of nerve-cells which can take on the duty of the injured cells, and act for them in receiving sensory, and discharging motor impulses.

It has already been pointed out that the function of any given nerve fibre depends on the relationships of its terminals. The fibre itself is merely a conducting agent. In somewhat the same way the functions of any given nerve-cell must depend on the number and character of its connections. If it be connected with a motorial end-plate in a muscle, it can only excite impulses that give rise to motion: if it be connected with a sensory terminal, it can only be a receiver of sensory impulses. But, in the grey matter of the spinal cord, and still more so in that of the cerebral cortex, we may assume that all the cells are in more or less intimate connection with innumerable other cells. In fact, we must imagine that the grey matter of both cord and brain is interwoven into a complex texture of fibrils and cells, no part of which is isolated from the rest, but all the elements form part of a continuous system, and within certain limits can subsidise each other's functions.

When we excise, cauterise or stimulate a given point of the complex cortex, we do not know in what way we interfere with the perfect action of that wonderful nervous nexus which controls the organism, for we can only judge of the effects we produce by results limited to those few functions the activity of which is obvious.

CHAPTER XXXVII.

REPRODUCTION.

Male and Female Generative Elements.

One of the chief characteristics of living beings is their power of reproduction ; that is to say, organisms can, under favourable conditions, form other individuals with lives and habits similar to their own.

In the lowest forms of animal life this propagation of species may take place by the division of a single cell : thus an amœba reproduces by the cleavage of its mass of protoplasm, separating the main body into two amœbæ. Such a method of reproduction is purely *asexual*, each individual having the intrinsic power of reproduction.

As we ascend the animal scale, we find that, just as other functions are executed by certain specially differentiated groups of cells, so reproduction is performed by certain collections of cells endowed with specific powers. Further, we find that the production of a new being requires the co-operation of two kinds of generative elements, each of which is produced by a distinct organ. In the higher organisms these reproductive elements are produced by different individuals of the same species, thereby dividing them into two sexes. This is termed *sexual reproduction.*

The sexual method of reproduction is met with in all the more highly developed forms of animal and vegetable life. The male organ produces active elements—the spermatozoa ; the female organ produces the ovum, which, when fertilised by the spermatozoa, develops *embryo.*

In mammalia the uterus is a most important subsidiary organ, as it becomes modified to allow of the development and growth of the embryo : its earlier functions, however, can be performed by other organs, as seen in cases of extra-uterine fœtation, when the ovum develops in some unusual situation, such as the Fallopian tube, or the abdominal cavity.

The *spermatozoa* are formed indirectly from the cells lining the tubuli seminiferi of the testicle. These cells, cubical masses of protoplasm, give rise to others (*spermatoblasts*), which form another layer and undergo rapid proliferation. The nuclei divide, and from each part arises the head of a spermatozoon, the body being developed

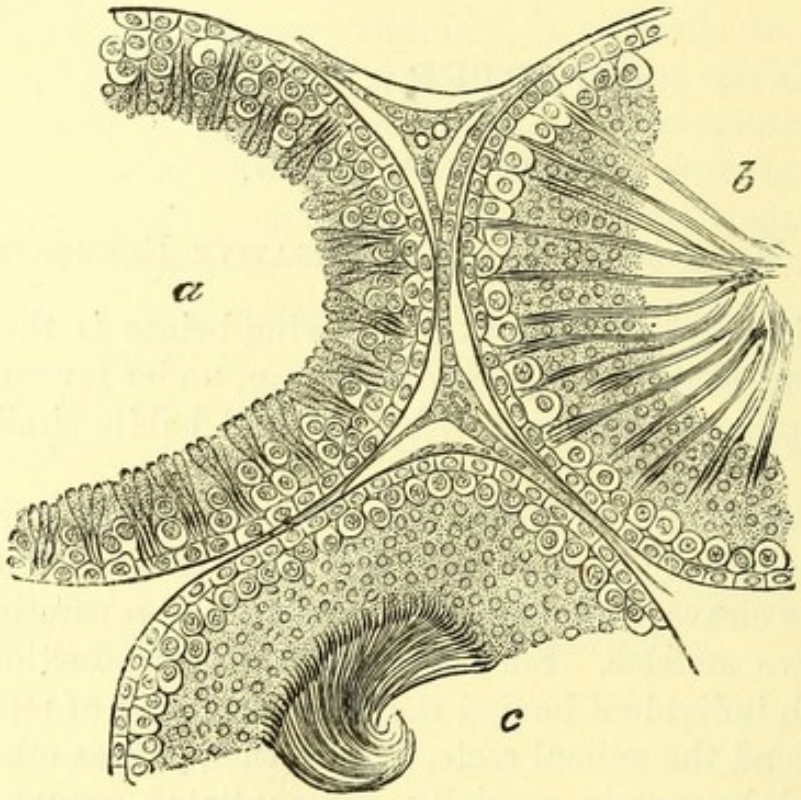


Fig. 264.—Section of the tubuli seminiferi of a rat. (Schäfer.)

a. Tubuli in which the spermatozoa are not fully developed.
b. Spermatozoa more developed. *c*. Spermatozoa fully developed.

from the protoplasm of the cell. The spermatic elements escape into the tubes, and pass down the *vasa deferentia* into the *vesiculæ seminales*, where they either undergo a retrograde change or are cast out of the body.

The *ovum* arises from the differentiation of a cell from the *germ-epithelium* covering the surface of the ovary. A group of these cells entering the periphery of the ovary, becomes there embedded in a kind of capsule derived from the surrounding areolar tissue of the stroma, and forms an immature *Graafian follicle*. A central cell grows rapidly to form the ovum, the rest increase in number to form the small cells of the granular tunic. As the follicle develops, it works its way towards the centre of the ovary, and subsequently approaches the periphery of the organ as a fully-developed Graafian follicle.

Microscopically, it is seen to be surrounded by a capsule, *tunica*

fibrosa, which is ill-defined from the stroma of the ovary in which it lies. Outside this a layer of capillary blood-vessels, *tunica vasculosa*,

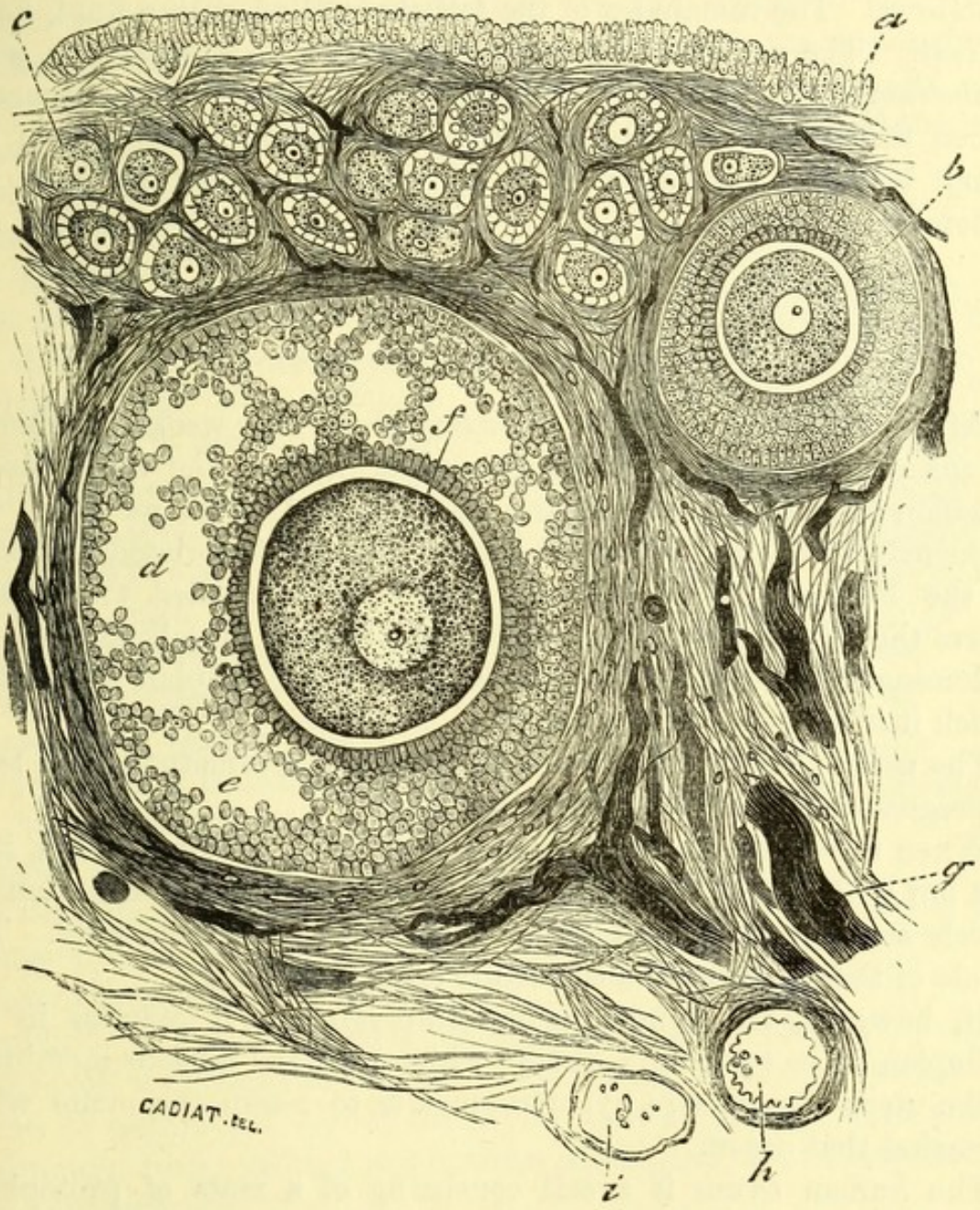


Fig. 265.—Section of the ovary of a cat, showing the origin and the development of Graafian follicles. (Cadiat.)

a. Germ-Epithelium.
b. Graafian follicle partly developed.
c. Earliest form of Graafian follicle.
d. Well-developed Graafian follicle.
e. Ovum.
f. Vitelline membrane.
g. Veins.
h, *i*. Small vessels cut across.

and to these two coats collectively the term *tunica propria* is applied.

Inside the tunica propria are granular cells of small size, which occupy a considerable space in the follicle; they are heaped up at

one spot round the ovum, which lies embedded in their midst. These cells receive the name of the *tunica granulosa*, and their projecting portion, which encircles the ovum, is called the *discus proligerus*. The remainder of the follicle is filled with a fluid, *liquor folliculi*. The surface of the ovary is covered by columnar cells, *germ-epithelium*, continuous with the endothelial cells of the peritoneum. When the follicle is fully matured, it lies at the periphery of the ovary beneath this layer of cells, which separates it from the abdominal cavity.

Menstruation and Ovulation.

After puberty, at intervals averaging about four weeks, the genital organs of the female become congested, and at the same time a Graafian follicle is ruptured and its contained ovum set free. Coincidently with the rupture of the follicle, the fimbriated extremity of the Fallopian tube becomes closely approximated to the spot where the follicle lies, so that the ovum instead of falling into the abdominal cavity, passes into the canal of the Fallopian tube, down which it is conveyed to the uterus.

The usual place for the ovum to meet the spermatozoa, and to be impregnated, is the Fallopian tube.

When the ovum reaches the uterus, if it be unimpregnated, it is cast out with the surface cells of the mucous membrane of the uterus, which are destroyed, and escape along with a sanious fluid. The whole of these phenomena constitute a menstrual act.

If, however, the ovum become impregnated, it remains in the Fallopian tubes some days, during which time the mucous membrane of the uterus becomes so hypertrophied as to retain the ovum when it reaches that organ.

The human ovum is a cell consisting of a mass of protoplasm enclosing a nucleus and nucleolus, and surrounded by a cell-wall. On its outer surface is an irregular layer of cells, the remains of that part of the tunica granulosa which encircled the ovum in the Graafian follicle. The cell wall of the ovum is called the *vitelline membrane* or *zona pellucida*, and the mass of granular protoplasm it encircles, the *vitellus* or yolk, and in this is a nucleus—the *germina vesicle*, which contains a nucleolus—the *germinal spot*.

Beneath the outer covering of calcareous material of the hen's egg there is a white membrane, which encloses a transparent albuminous substance known as the white of egg. Inside this is a yellow fluid

mass, the yolk, surrounded by a delicate membrane, *vitelline membrane*. The yolk is made up of two varieties of material of different shades of colour, the white and the yellow yolk. Of these the yellow forms the greater part, the white being arranged in thin layers, which separate the yellow yolk into strata. In the centre of the yolk it forms a flask-shaped mass, with its neck turned to the upper surface, upon which a portion of the yolk rests called the *cicatricula*. This cicatricula, which lies between the vitelline membrane and the white yolk, is the active growing part of the egg, and out of it is developed the chick and the embryonic membranes.

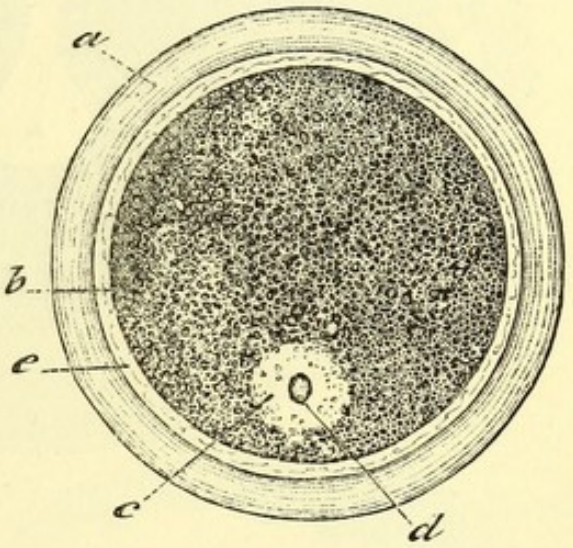


Fig. 266.—Ovum. (Robin.)

a. Zona pellucida or vitelline membrane.
b. Yolk.
c. Germinal vesicle or nucleus.
d. Germinal spot or nucleolus.
e. Interval left by the retraction of the vitellus from the zona pellucida.

Extending through the albumin from the vitelline membrane to the ends of the egg are two twisted membranous cords—the *chalazæ*, which fix and protect the delicate yolk from shocks, but allow it to rotate, so that the cicatricula is always the uppermost part of the yolk when the egg is on its side.

The main structural differences between the human ovum and that of a fowl are apparent from the above description: the essential peculiarity of the development of the hen's egg is that only a portion of the yolk is engaged in the formation of the first signs of the chick and its membranes, by far the greater part of the egg, both yolk and albumin, being utilised as nourishment during the subsequent stages of development.

After the egg has been laid, it obtains no help from the outside world, except the oxygen of the air and the heat of the mother's body; it is, as it were, fenced in with a protecting membrane, garrisoned with the quantity of provisions required, and by the warmth of the hen's body stimulated to growth and activity.

The whole of the human ovum, on the other hand, undergoes segmentation and differentiation in the primary formation of the embryo, which subsequently is supplied with the necessary nourishment from the maternal circulation. The life and growth of the human embryo

depend upon supplies from the mother, the ovum not having within itself any store of nutrient material.

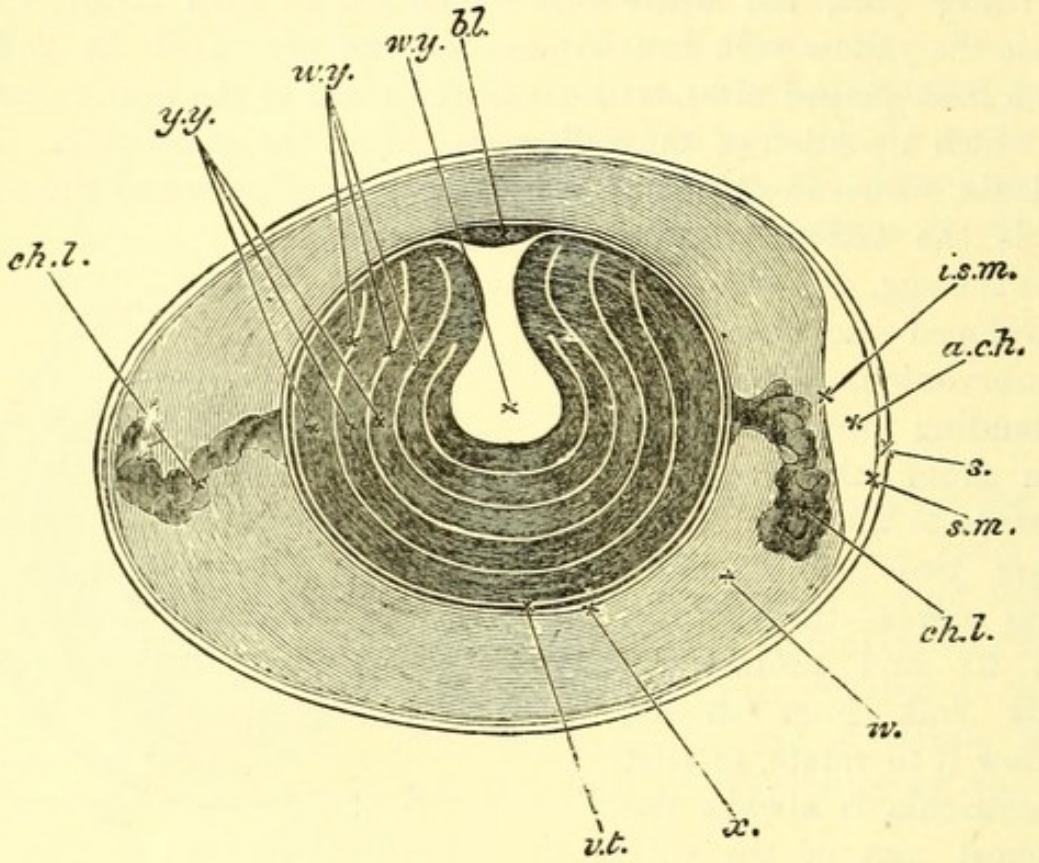


Fig. 267.—Diagram of a section of an unimpregnated fowl's egg. (From Foster and Balfour, after Allen Thomson.)

bl. Blastoderm or cicatricula.
w.y. White yolk.
y.y. Yellow yolk.
ch.l. Chalaza.
i.s.m. Inner layer of shell membrane.
s.m. Outer layer of shell membrane.
s. Shell.
a.ch. Air space.
w. The white of the egg.
vt. Vitelline membrane.
x. The denser albuminous layer which lies next to the vitelline membrane.

Changes in the Ovum subsequent to Impregnation.

The first changes in the ovum independent of impregnation consist in the shrinking of the yolk from the vitelline membrane, and the extrusion from it of certain granular bodies which lie between it and the vitelline membrane, and are called the *polar globules*. The germinal spot and germinal vesicle also disappear, and are said, by some observers, to form these polar globules. After the union of the male and female elements, a new nucleus appears in the vitellus which forms what is called the *segmentation sphere*. This divides at first into two segments, then into four, eight, sixteen, and so on, until a large mass of cells occupies the yolk. To

this condition the name of *morula* is given, from its supposed likeness to a mulberry. Fluid now collects among the cells, and separates some of them from the others, and they arrange themselves

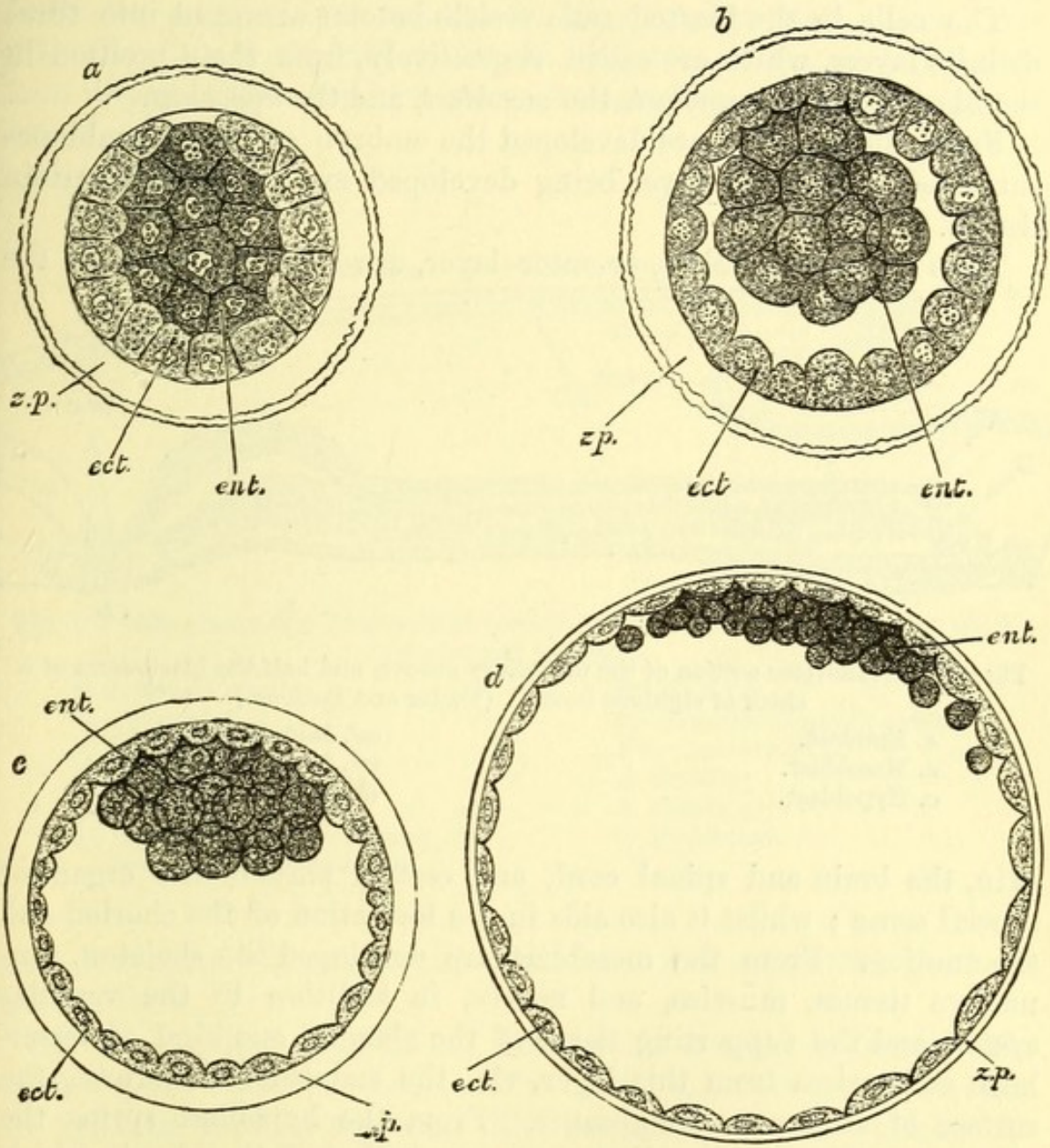


Fig. 268.—Sections of the ovum of a rabbit, showing the formation of the blastodermic vesicle. (E. Van Beneden.)

a, *b*, *c*, *d*, are ova in successive stages of development. *zp*. Zona pellucida. *ect*. Ectomeres, or outer cells. *ent*. Entomeres, or inner cells.

into an outer and inner layer, consisting of different kinds of cells. The inner cells finally become aggregated at one part of the ovum in contact with the outer cells. The ovum now receives the name of the *blastodermic vesicle*.

In the hen's egg the cleavage is confined to the cicatricula or

blastoderm, and does not include the rest of the yolk. From the fact that the cleavage of the yolk is only partial, such an ovum receives the name of *meroblastic*. The human ovum, which undergoes complete segmentation, is called *holoblastic*.

The cells in the blastodermic vesicle become arranged into three definite layers, which are called respectively, from their position in the blastoderm, the *epiblast*, the *mesoblast*, and the *hypoblast*.

From these layers are developed the embryo and the membranes surrounding it, each layer being developed exclusively into certain tissues.

Thus from the epiblast, or outer layer, arise the epidermis of the

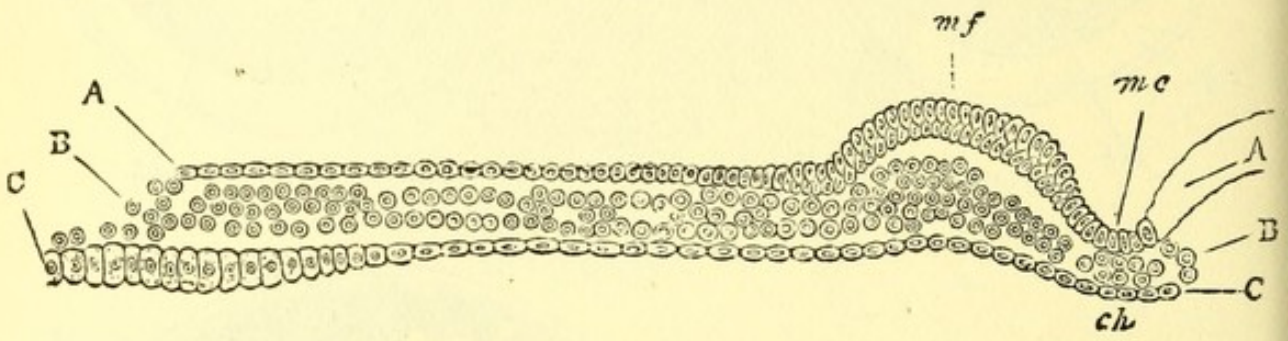


Fig. 269.—Transverse section of the medullary groove, and half the blastoderm of a chick of eighteen hours. (Foster and Balfour.)

A. Epiblast.
B. Mesoblast.
C. Hypoblast.
mf. Medullary fold.
mc. Medullary groove.
ch. Notochord.

skin, the brain and spinal cord, and certain parts of the organs of special sense ; whilst it also aids in the formation of the chorion and the amnion. From the mesoblast are developed the skeleton, connective tissues, muscles, and nerves, in addition to the vascular system and the supporting tissue of the glands ; one kind of tessellated cells arises from this layer, viz., the endothelium, forming the surface of all serous membranes. From the hypoblast spring the epithelial lining of the alimentary canal, that of the glands which are diverticula from it, and of the lungs ; it also forms the lining membrane of the allantois and yolk sac.

The blastoderm of the hen's ovum, which is comparatively easily studied, consists of a small clear central portion, called the *area pellucida*, from which the body of the chick arises. Surrounding the area pellucida is a much larger zone, which appears less transparent ; this, the *area opaca*, is devoted to the formation of the membranes.

The embryo is developed from the rest of the blastoderm in the following manner. At the front of the area pellucida a fold, or

dipping in of the blastoderm takes place; this consists of a projecting part above and a groove below, and constitutes the *cephalic*, or head fold. The upper projecting portion of the fold tends to grow forwards, whilst the groove grows gradually backwards. Later on, another fold appears at the posterior part of the area pellucida, this is the tail fold. At the sides of the area pellucida folds appear, which tend to grow downwards and inwards so as to

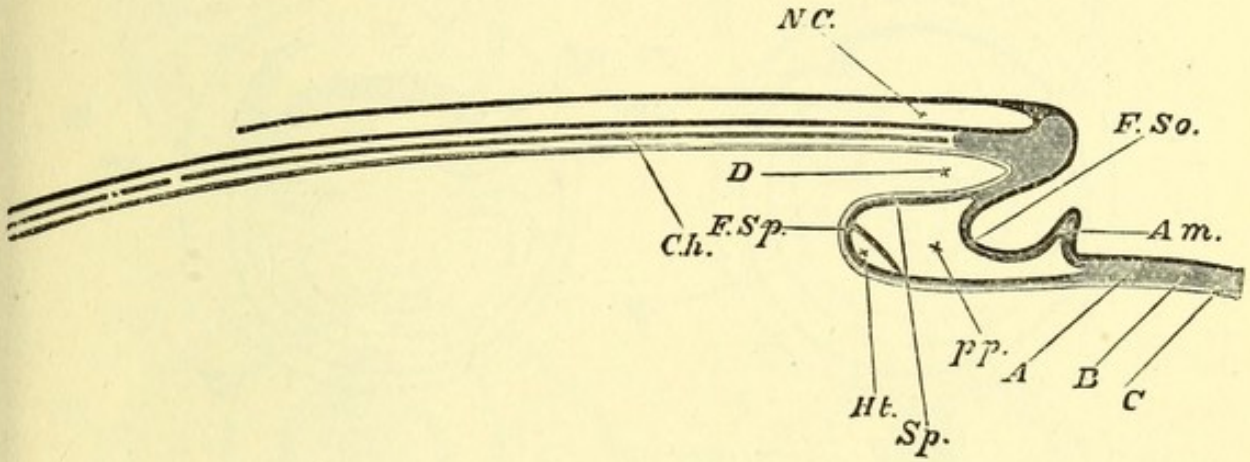


Fig. 270.—Diagrammatic longitudinal section through the axis of an embryo chick. (Foster and Balfour.)

N.C. Neural canal.
Ch. Notochord.
D. Foregut.
F.So. Somatopleure.
F.Sp. Splanchnopleure.
Sp. Splanchnopleure forming the lower wall of the foregut.
Ht. Heart.
pp. Pleuroperitoneal cavity.
Am. Amniotic fold.
A. Epiblast.
B. Mesoblast.
C. Hypoblast.

reach the under surface of the blastoderm and unite with the head and tail folds.

By the approximation of all these folds a canal is formed—*the embryonal sac*—which is closed above by the main portion of the area pellucida, in front by the head fold, behind by the tail fold, at the sides by the lateral folds, whilst below it is open to the vitellus. This canal ultimately becomes subdivided into an inner tube, the alimentary tract, and an outer one, which forms the body walls, the final place of union of the folds being marked by the umbilicus. It must be clearly understood that these primary folds which form the embryo include in their layers the epiblast, the whole thickness of the mesoblast, and the hypoblast, whereas the folds giving rise to the membranes do not comprehend all these layers.

Formation of the Membranes.

(1.) *The Amnion.*—The mesoblast around the embryo becomes thickened, and is split into two distinct layers; this cleavage is at first confined to the neighbourhood of the embryo, but gradually spreads over the whole blastoderm.

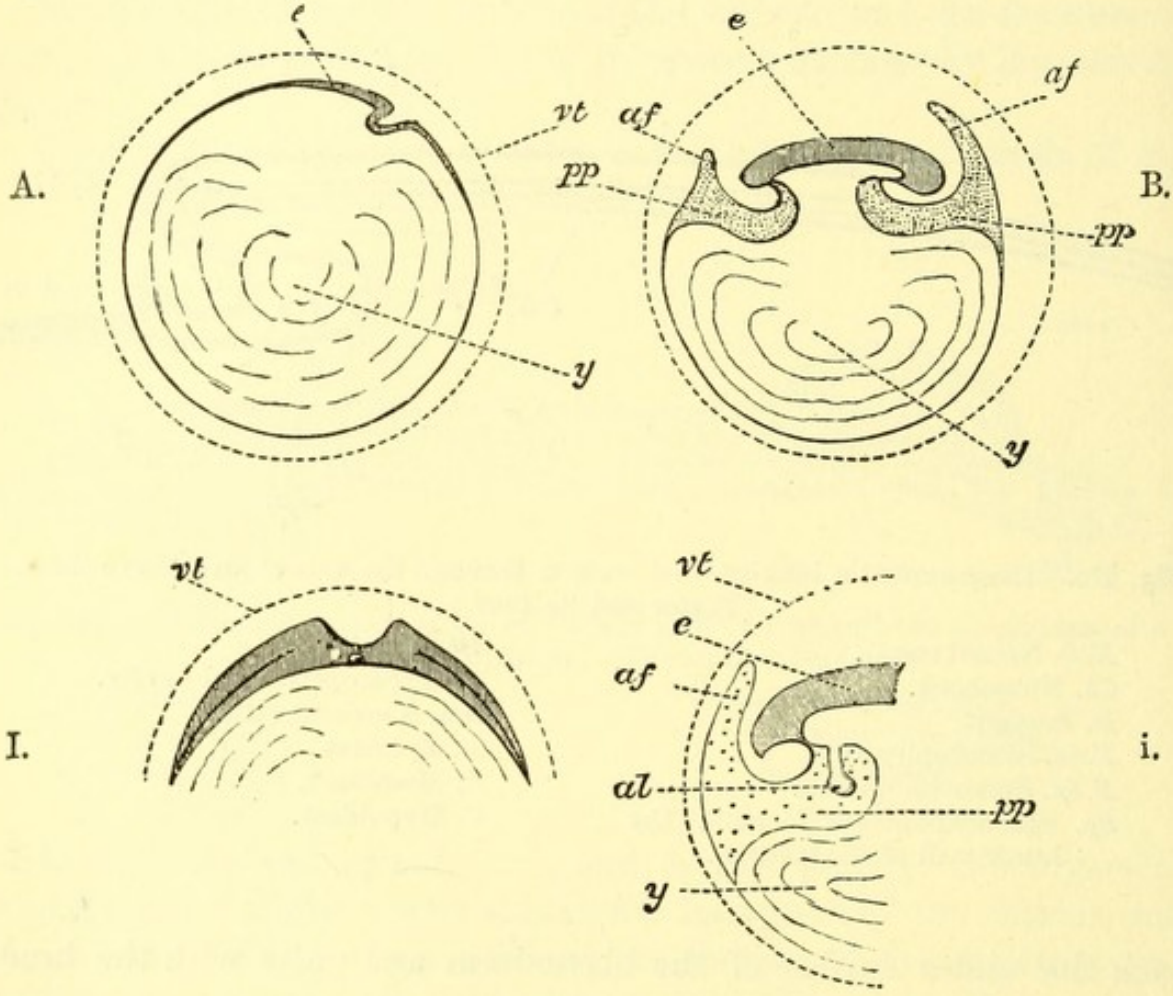


Fig. 271 and the two following woodcuts are diagrammatic views of sections, through the developing ovum, showing the formation of the membranes of the *chick*. (Foster and Balfour.)

A, B, C, D, E, and F are vertical sections in the long axis of the embryo at different periods, showing the stages of development of the amnion and of the yolk-sac.

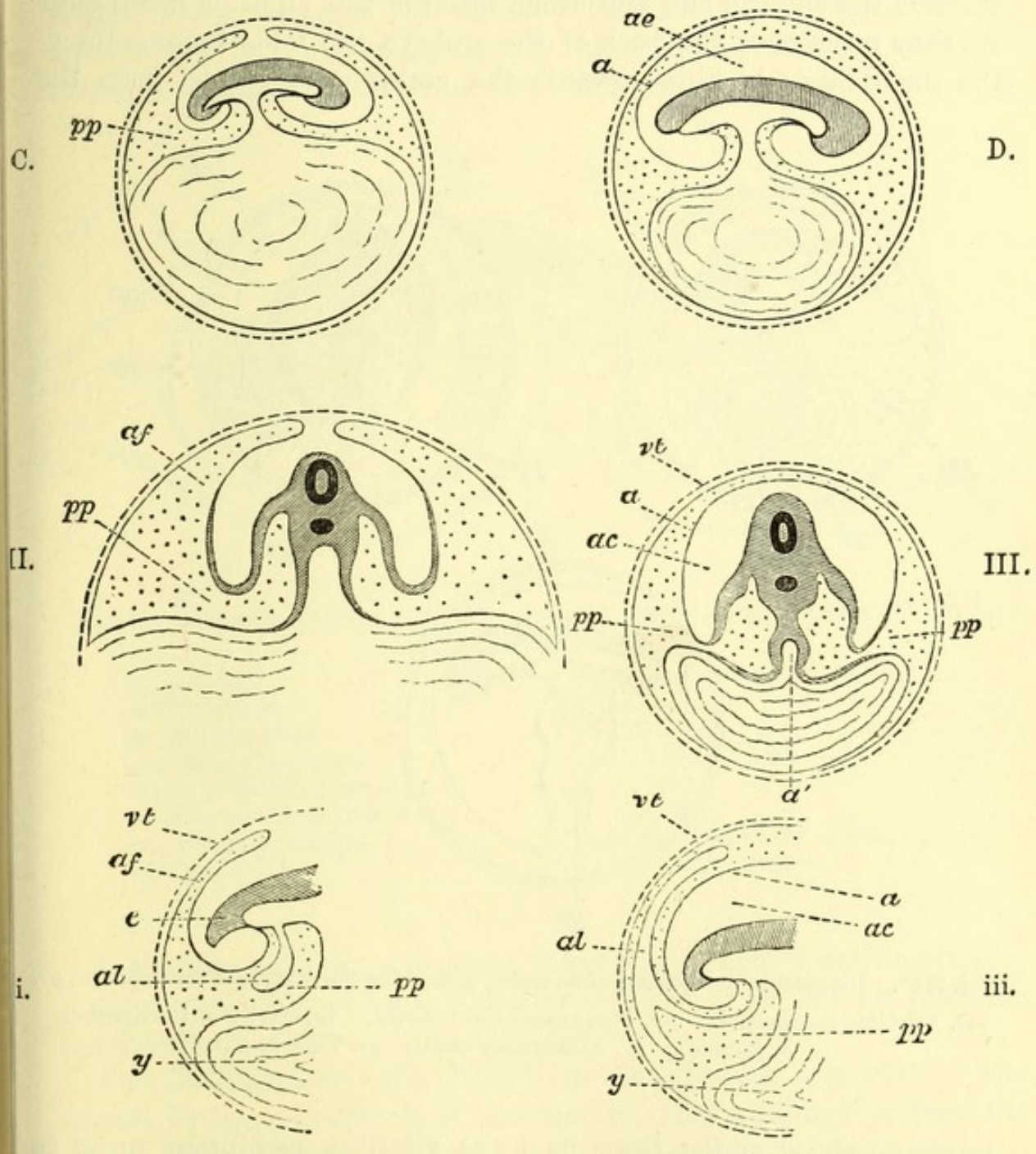
I., II., III., and IV. are transverse sections at about the same stages of development.

i., ii., and iii. give only the posterior part of the longitudinal section, to show three stages in the formation of the allantois.

e. Embryo.
y. Yolk.
pp. Pleuroperitoneal fissure.
vt. Vitelline membrane.
af. Amniotic fold.
al. Allantois.

The upper of these two layers of the blastoderm receives the name of the *somatopleure*, and is engaged in the formation of the body walls of the embryo and the amnion. The lower one is called the

splanchnopleure, and forms the walls of the alimentary canal, the allantois, and the yolk-sac. The space intervening between these layers is called the pleuroperitoneal cavity. At a point in front of



e. Embryo.
a. Amnion.
a'. Alimentary canal.
vt. Vitelline membrane.

af. Amniotic fold.
ac. Amniotic cavity.
y. Yolk.
al. Allantois.

the cephalic fold, an upward projection of somatopleure takes place, conveying with it the overlying epiblast. Along the sides of the embryo and behind the caudal fold, projections of the somato-

pleural mesoblast and epiblast also occur. Thus folds are developed consisting of somatopleural mesoblast and of epiblast, which tend to grow upwards and meet over the back of the embryo. These are the amniotic folds, and each presents two surfaces, one looking towards the embryo and the other towards the vitelline membrane. As they meet over the back of the embryo the folds become fused, the membranes looking towards the embryo joining to form the

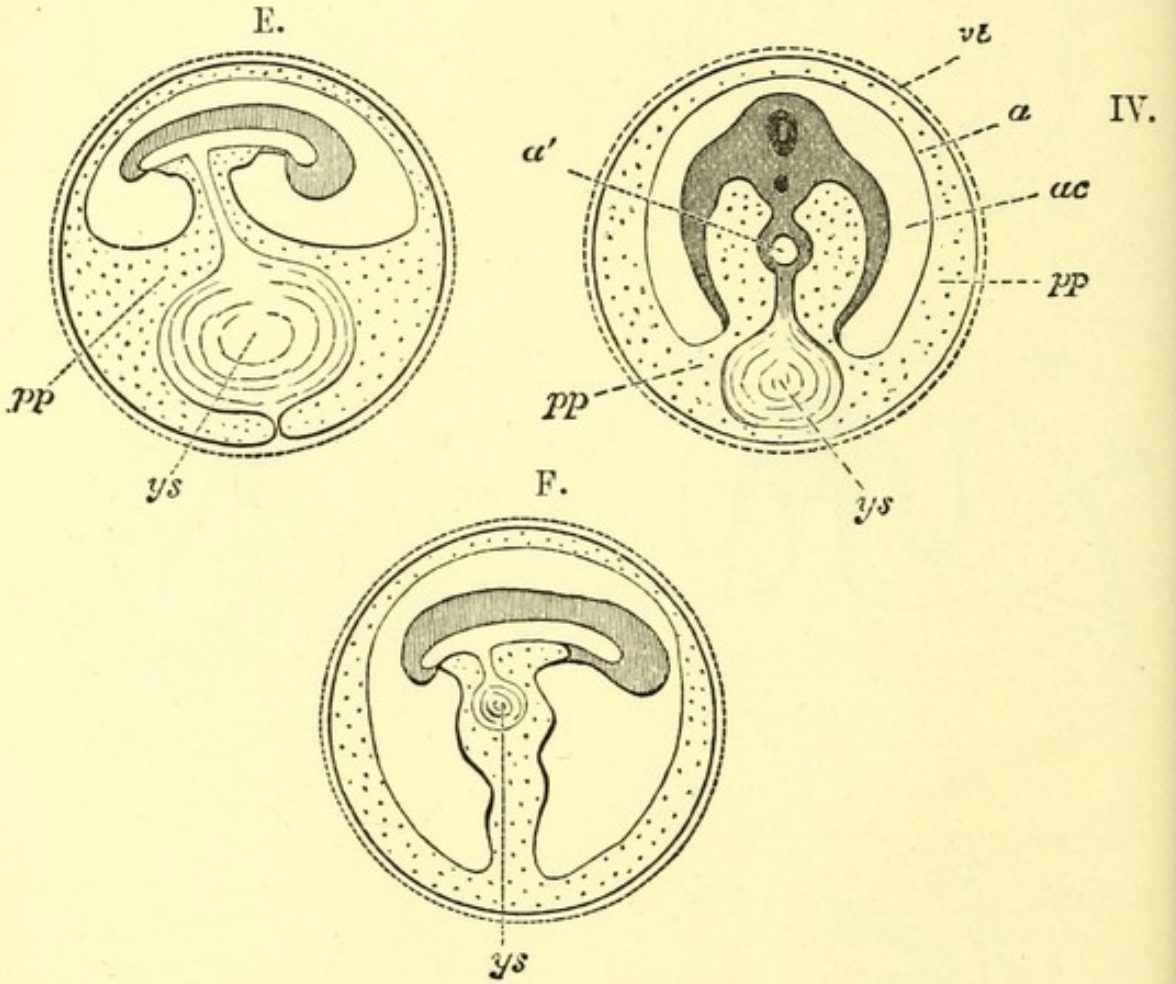


Fig. 271*.—Diagrammatic sections of an embryo, showing the destiny of the yolk-sac, *ys*. *vt*. Vitelline membrane. *pp*. Pleuroperitoneal cavity. *ac*. Cavity of the amnion. *a*. Amnion. *a'*. Alimentary canal. *ys*. Yolk-sac.

amnion proper, whilst those next the vitelline membrane unite to form the *false amnion*, which, separating from the amnion proper, retires towards the vitelline membrane, with which it unites to form the primitive chorion.

The proper amnion then is a sac formed of an outer layer derived from the mesoblast and an inner layer derived from the epiblast. The false amnion likewise consists of mesoblast and epiblast, but here the epiblast is external. The amnion proper is continuous with

the skin of the embryo, and when the fœtus is mature, the connection may be traced by the umbilical cord, round which it forms a sheath continuous with the skin at the umbilicus. This membranous sac enlarges, and in mammalia eventually becomes the large bag of liquid which contains the fœtus. The *amniotic liquid* is of low specific gravity, consisting mainly of water containing traces of nitrogenous matter, phosphates and chlorides.

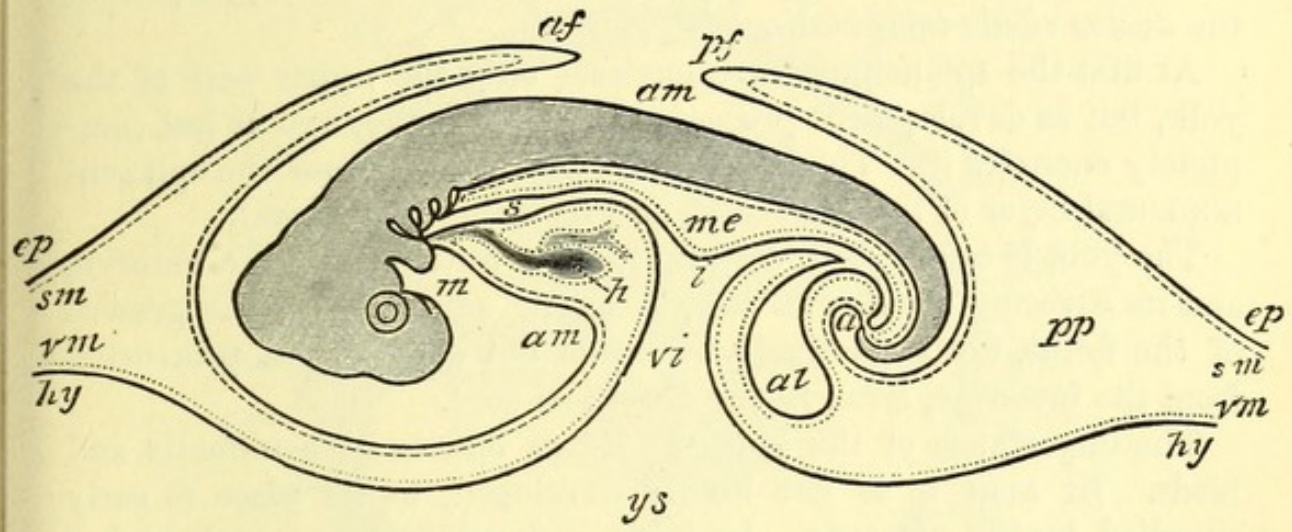


Fig. 272.—Diagrammatic longitudinal section of a chick on the fourth day. (Allen Thomson.)

ep. Epiblast.
hy. Hypoblast.
sm. Somatopleure.
v.m. Splanchnopleure.
af, *pf*. Folds of the amnion.
pp. Pleuroperitoneal cavity.
am. Cavity of amnion.
al. Allantois.
a. Position of the future anus.
h. Heart.
i. Intestine.
vi. Vitelline duct.
ys. Yolk.
s. Foregut.
m. Position of the mouth.
me. The mesentery.

It contains albumin and some other nitrogenous constituents, and a minute quantity of urea, which is thought to be derived from the fœtal kidneys.

This fluid preserves the child from the effects of any jolts or jars caused by the movements of the mother, and similarly protects the uterus of the mother by acting as a buffer between the fœtus and the uterine wall. Before delivery it helps to dilate the os uteri, so that when the amnion is ruptured the head of the fœtus occupies the opening which has been gradually made by the fluid wedge. The outer part of the amniotic membrane, derived from the mesoblast, is of a tougher character than the inner epithelial layer, possesses muscular fibre and is capable of rhythmical contractions.

(2.) *The Yolk-sac* is that part of the blastoderm which grows and

envelops the yolk, which previously was only surrounded by the vitelline membrane. After the mesoblast has split into two layers, the splanchnopleure becomes bent inwards at a point some distance from its origin, carrying with it the hypoblast. By this curve an upper constricted canal is differentiated from the large lower cavity. This upper canal becomes eventually the alimentary tract, the lower cavity the yolk-sac, whilst the constricted portion leading from one to the other is the canal leading from the intestine to the yolk, called the *ductus vitello-intestinalis.*

At first the splanchnopleure encloses only the upper part of the yolk, but as development proceeds it grows around, and at last completely encircles it. The yolk-sac is thus derived from the splanchnopleural layer of the mesoblast, and its lining hypoblast.

The yolk is continually used up for the nutrition of the embryo, and its covering shrinks in size, becoming smaller with the growth of the fœtus, until eventually it forms but a shrivelled protrusion from the intestine, lying in the umbilical cord.

The importance of the yolk-sac differs largely in mammalia and birds. In man it is not highly developed, as its place is early supplied by the placenta. In birds it develops to a much higher degree, being the seat of a special circulation, which carries nourishment from the yolk to the chick. The vessels are developed in the mesoblastic portion of the membrane, and are called the *omphalo-mesenteric vessels*, which convey blood to and from the primitive heart.

(3.) *The allantois*, or urinary vesicle, in the chick is of importance, as the vessels developed in it are used for respiratory purposes, being spread out beneath the porous shell. In the mammalian embryo it is still more important, as it is the seat of the circulation, which performs the chief function of the fœtal placenta. The allantois arises at the tail of the embryo, as a budding outwards of a portion of the splanchnopleure forming the wall of the primitive intestine. It is lined by hypoblast, and projects into the pleuro-peritoneal cavity. As it grows away from the embryo it extends between the layers of the true and false amnion and approaches towards the vitelline membrane, but remains connected to the intestine by a narrow tube. When it reaches the periphery of the ovum, it spreads over the chorion as a complete lining, and sends processes into the villi of that organ. It becomes chiefly developed at that part of the chorion which is opposite the *decidua serotina* of the mother. In the mesoblastic layer of the allantois blood-vessels arise which are connected with large trunks, proceeding from the

primitive aortæ, called the umbilical arteries; these will, however, be further described when treating of the fœtal placenta.

As the fœtus becomes developed, the part of the allantois in connection with the body becomes gradually obliterated. A part of it remains as the urinary bladder, and the rest forms a fibrous cord,

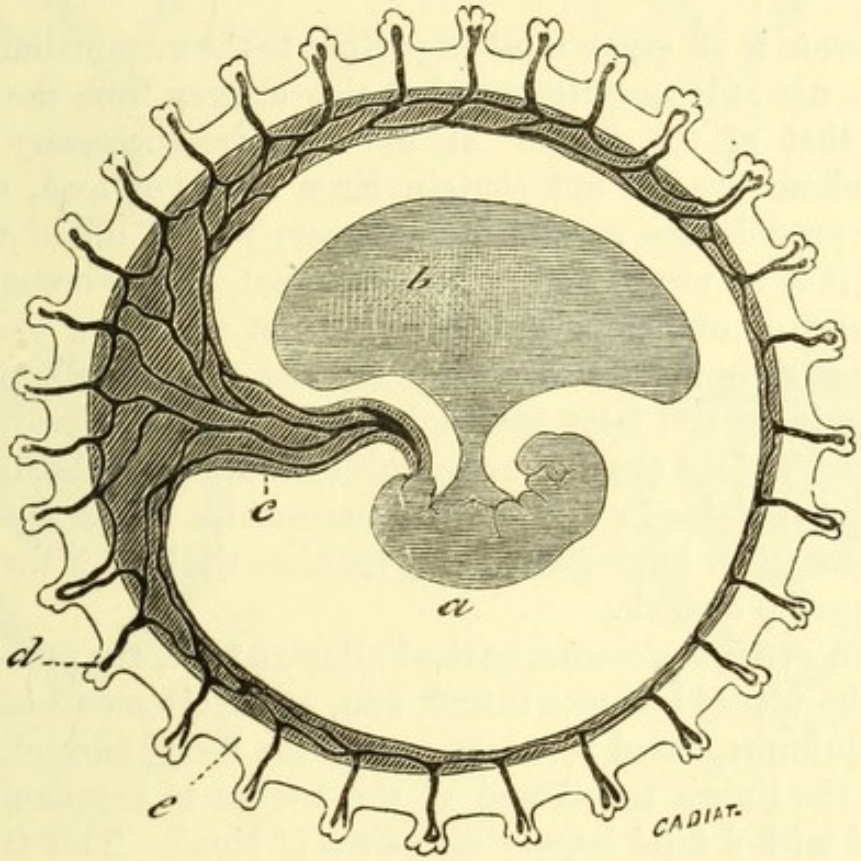


Fig. 273.—Diagram of an embryo, showing the relationship of the vascular allantois to the villi of the chorion. (Cadiat.)

a. Lies in cavity of the amnion under the embryo. *b*. Yolk-sac. *c*. Allantois.
d. Vessels of the allantois dipping into the villi of the chorion. *e*. Chorion.

which runs from the apex of the bladder to the umbilicus, and is known as the *urachus*.

(4.) *The Chorion* is the external covering of the ovum. At first it consists simply of the zona pellucida or vitelline membrane, and then it is called the primitive chorion. Later it is supplemented by that part of the somatopleure removed from the embryo in the process of forming the amnion. This blends with the primitive chorion and strengthens it, and while lying beneath the zona pellucida, receives the name of the subzonal membrane. The chorion at first is a smooth membrane, but villous processes early grow out from it. These villi are chiefly developed at its upper part, where they aid in the formation of the fœtal placenta.

The allantois, when it has spread over the chorion, becomes blended with this membrane, and fills the villous processes with the blood-vessels it contains.

The Placenta.

The placenta is an organ most important to the mammalian embryo. It conveys not only nourishment but also oxygen from the maternal blood to that of the fœtus. It is, of course, necessary that the animals whose ova do not contain large stores of food, should in some way provide the substances necessary for the life of their embryo, and it is by means of the placenta that this is brought about. The embryo of oviparous animals does not require a placenta for its nutrition, since there is inside the egg a large store of highly nutritious albuminous and fatty materials ; the shell is pervious to air, and the chick's blood can in the allantois be oxidised by the air directly. A bird's egg contains in itself all the necessaries which the placenta supplies, and when impregnated only requires the heat of the mother's body to develop a chick.

While an ovum is descending the Fallopian tube, the mucous membrane of the uterus becomes turgid, and, as before mentioned, if the ovum be unimpregnated it is cast out of the body, part of the substance of the lining membrane of the uterus is desquamated and discharged with a fluid largely composed of blood. This takes place approximately every four weeks, and hence is called menstruation. If the ovum be impregnated, however, the mucous membrane of the uterus not only becomes turgid, but its cells proliferate, and considerable thickening of the tissue takes place. The mucous membrane is then called the *decidua.* When the ovum reaches the uterus it ordinarily becomes embedded in that part of the decidua which occupies the fundus of the uterus. The decidua here grows excessively, and becomes much thickened, and on either side of the ovum a projection is sent from the decidua which meets below the ovum, and completely encircles it.

The name *decidua vera* is given to the membrane lining the general cavity of the uterus, whilst that part lining the fundus, to which the ovum is attached, is called the *decidua serotina*, and its processes surrounding the ovum receive the name of the *decidua reflexa.*

The placenta is developed from two sources, one arising from the membranes of the fœtus, and the other belonging to the mother.

Relation of the fœtal to maternal placentæ.—The maternal part

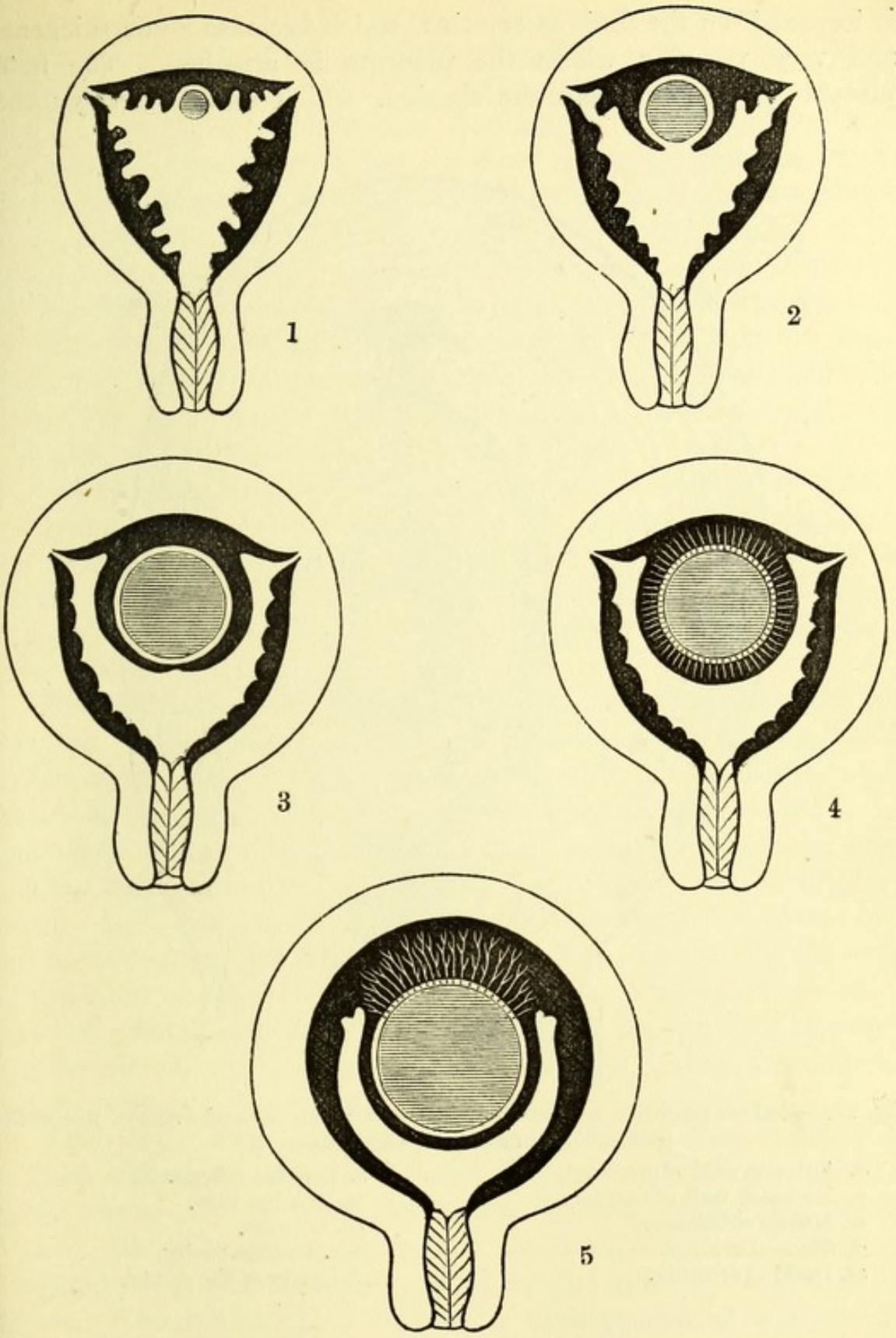


Fig. 274.—Series of diagrams representing the relationship of the decidua to the ovum at different periods. The decidua are coloured black, and the ovum is shaded transversely. In 4 and 5 the vascular processes of the chorion are figured (copied from Dalton).

1. Ovum entering the congested mucous membrane of the fundus—decidua serotina.
2. Decidua reflexa growing round the ovum.
3. Completion of the decidua around the ovum.
4. General growth of villi of the chorion.
5. Special growth of villi at placental attachment, and atrophy of the rest.

is formed from the decidua serotina, which becomes much thickened and very vascular where the placenta is attached. The fœtal placenta is derived from the chorion, which sends out a number

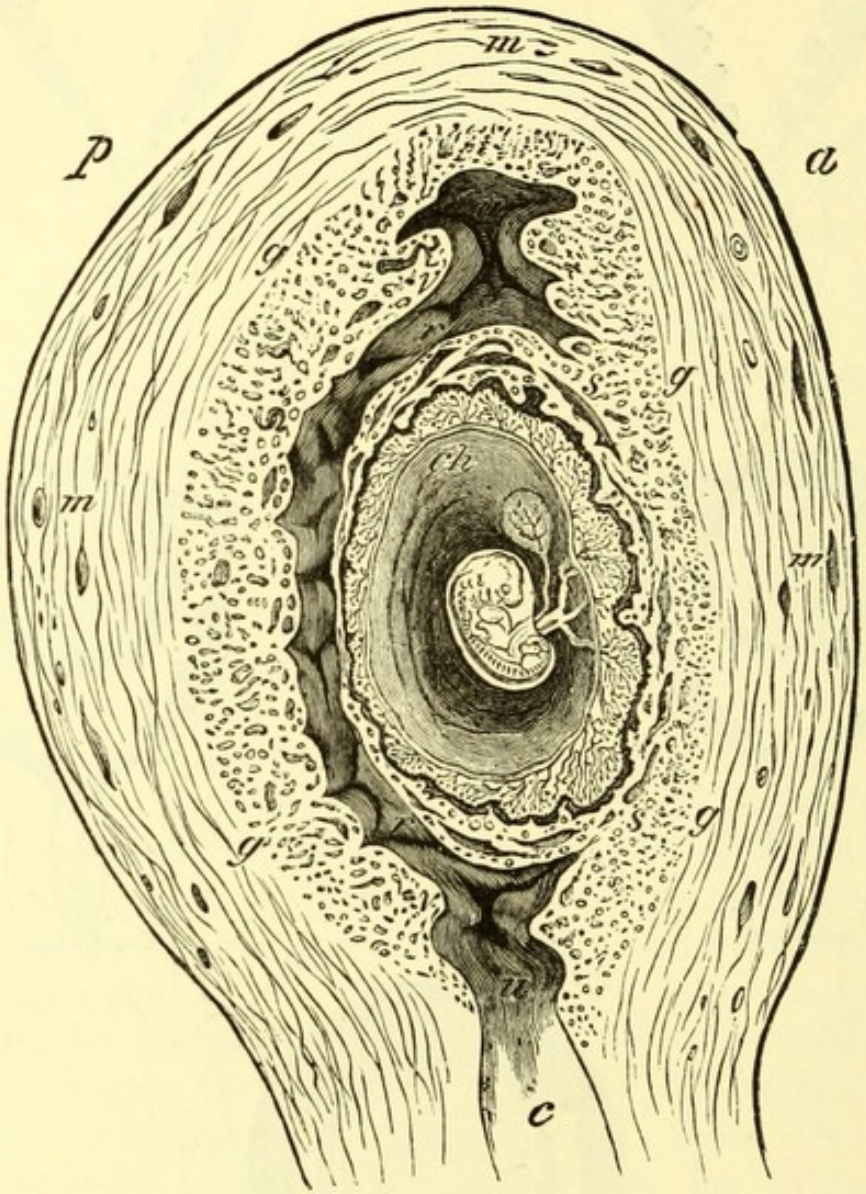


Fig. 275.—Antero posterior section through a gravid uterus and ovum of five weeks (semi-diagrammatic). (Allen Thomson.)

a. Anterior wall of uterus.
p. Posterior wall of uterus.
m. Muscle substance.
g. Glandular layer.
ss. Decidua serotina.
r. Decidua reflexa.
v. Decidua vera.
ch. Chorion.
u.u. Uterine cavity.
c. Cavity of the cervix.

of finger-like processes, which sub-divide, and into which the allantois, as it spreads over the chorion, sends prolongations. The mesoblastic layer of the allantois gives rise to the capillaries which are in these processes. The capillaries spring from the branches of the umbilical arteries which pass along the umbilical cord to reach

the chorion. The vessels of the decidua serotina or maternal placenta end in large sinuses, lined by endothelial cells. The blood is carried to these sinuses by the uterine arteries, and from them by the uterine veins. The walls of the sinuses are provided with unstriped muscular tissue, which can close the inlets from the arteries, and thus shut out the blood. The villi of the fœtal placenta, dipping into these uterine sinuses, are covered with a single layer of thin scaly cells, so that the fœtal blood is only separated from the maternal by the walls of the capillaries and these thin cells, and thus the interchange of nutrient materials and gas readily go on between them; it is very similar to the conditions of the lung alveoli, where the blood is separated from the air with which it interchanges gases by the cells of the capillary wall and of the lung alveolus.

Though the capillaries of the fœtus are in such close relation to the blood of the mother, it must be distinctly understood that there is no direct communication between the vessels of the fœtus and those of the mother, and therefore it is not possible to inject the vessels of the mother through those of the fœtus, or *vice versâ*.

The nutrient materials from the maternal blood together with oxygen diffuse through the walls of the fœtal capillaries, the effete matter, on the other hand, passing from the capillaries to the blood in the veins which surrounds and bathes these vessels. The placenta increases with the growth of the fœtus till shortly before birth, when it is said to undergo a certain amount of degeneration. It is cast out of the uterus after the expulsion of the fœtus with the membranes attached to it. It is, however, only the superficial layer of the maternal placenta (which is intimately connected with the fœtal placenta) that is cast off, the deeper layer remaining in the uterus, and undergoing various changes during the reduction of this organ to its normal size.

After ligature of the umbilical cord, the intimate relationships of the maternal and fœtal circulation cease, and it is thought that this causes the inlets of the uterine sinuses to contract, so that when the placenta separates from the uterine walls, the arterioles leading to the sinuses are contracted and possibly occluded with clots. The uterine blood current is thus prevented from escaping into the uterine cavity after parturition, and causing profuse hæmorrhage.

The uses of the placenta may be briefly summed up as—

(1) *Alimentary*, as it supplies the place of the organs of digestion by supplying the fœtal blood with nutritive material.

(2) *Respiratory*, as it performs the function of the lungs, the fœtal blood receiving oxygen from the oxyhæmoglobin of the mother, to which it gives up its CO_2.

(3) *Excretory*, as it does duty for the kidneys, removing the urea, &c., from the fœtal blood.

CHAPTER XXXVIII.

DEVELOPMENT OF THE SPECIAL SYSTEMS.

Development of the Vertebral Axis.

The earliest evidence of the differentiation of the blastoderm consists in the appearance of the *primitive streak* which forms the first sign of the embryo. This is a line which appears near what is to be the tail end of the embryo, and runs forwards. This primitive line or streak is due to the thickening of the mesoblast, and it becomes converted into a groove by a depression appearing in its centre, forming the *primitive groove*. This extends in a forward direction, but never reaches the head fold of the embryo, which, in the chick, appears a few hours after the formation of the primitive groove.

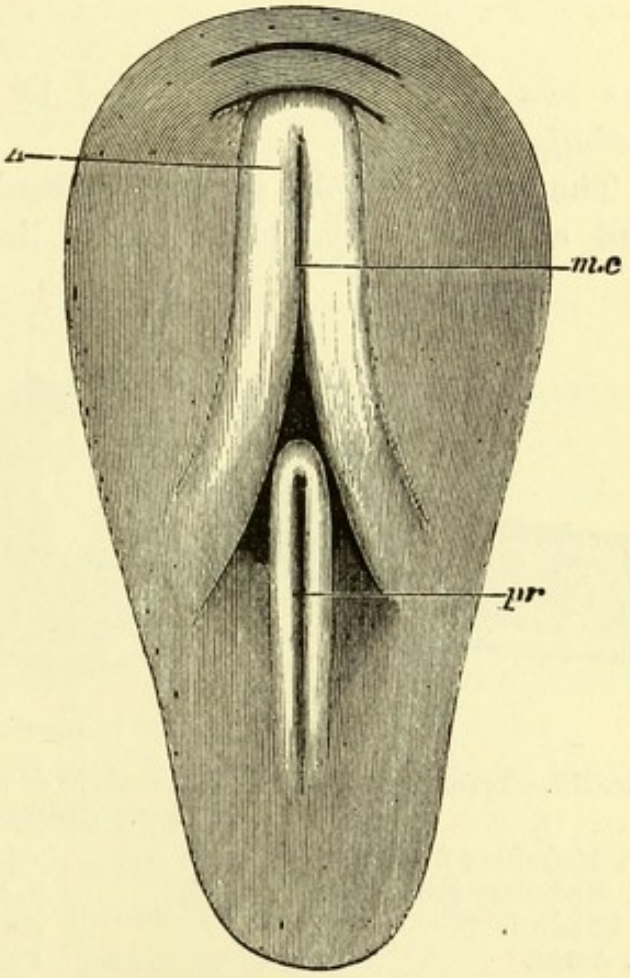


Fig. 276.—View of the area pellucida of a chick of eighteen hours seen from above. (Foster and Balfour).
A. Medullary folds.
mc. Medullary groove.
pr. Primitive streak and groove.

In front of the primitive groove, and stretching backwards to overlap it at the sides, arise two folds of the epiblast, called the laminæ dorsales or the *medullary folds*.

These are elevations of the epiblast, beneath which the mesoblast is thickened. They arise in front, where they are joined immediately

behind the head fold, whilst posteriorly they diverge, and passing on either side of the primitive groove, gradually become lost. Between

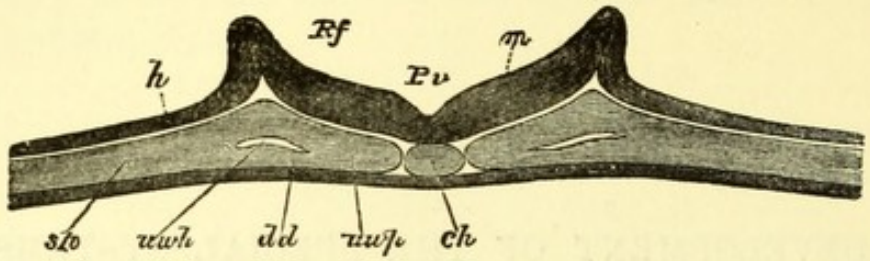


Fig. 277.—Transverse section of the embryo of a chick at the end of the first day. (Kölliker.)

sp. Mesoblast
d.d. Hypoblast.
m. Medullary plate.
h. Epiblast.
Pv. Medullary groove.
Rf. Medullary fold.
ch. Chorda dorsalis.
uwp. Proto-vertebral plate.
uwh. Division of mesoblast.

the two folds is a furrow lined by epiblast, which is called the *medullary groove.*

The medullary folds growing upwards, turn in towards one another, and eventually coalesce at their line of meeting, converting the

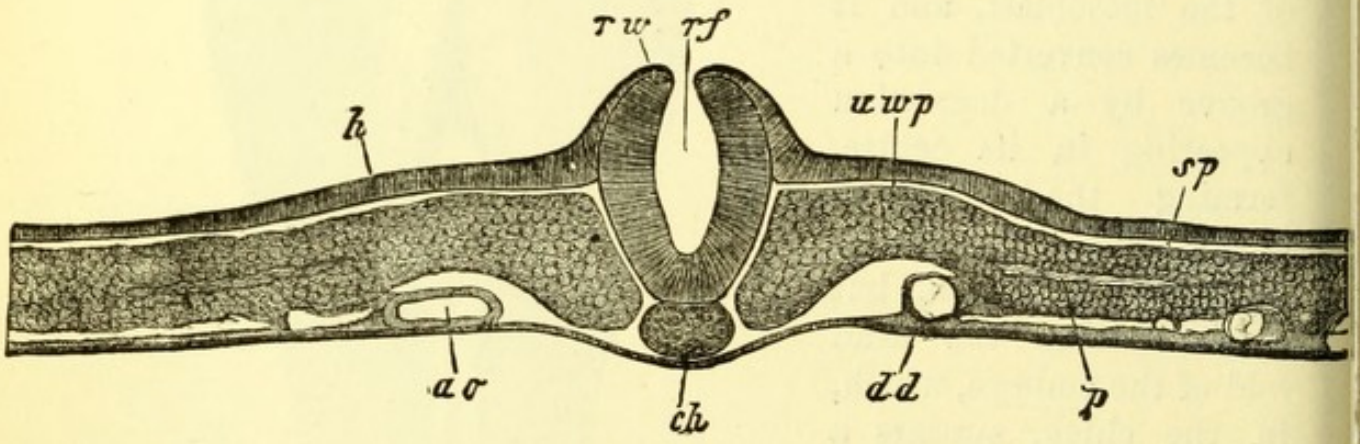


Fig. 278.—Transverse section of an embryo of a chick at the latter end of the second day. (Kölliker.)

rw. Medullary fold.
rf. Medullary groove.
h. Epiblast.
ao. Aorta.
dd. Hypoblast.
p. Pleuroperitoneal cavity.
sp. External plate of mesoblast dividing.
uwp. Proto-vertebral plate.

medullary groove into a channel—the *medullary canal;* this union of the folds takes place from before backwards.

The medullary canal thus formed lies in the axis of the embryo on the uncleft mesoblast; it is covered in superficially by several layers of epiblastic cells, which also line its walls. The canal is the earliest representative of the nervous centres, and eventually becomes

the brain and spinal cord. The front part of the canal, when completely closed in, becomes dilated into a bulb, thus forming the earliest indication of the brain. The hind part of the medullary groove remains unclosed considerably later than the fore part. It gradually becomes converted into a canal at the tail end, and as it extends backwards obliterates the primitive streak and groove, which

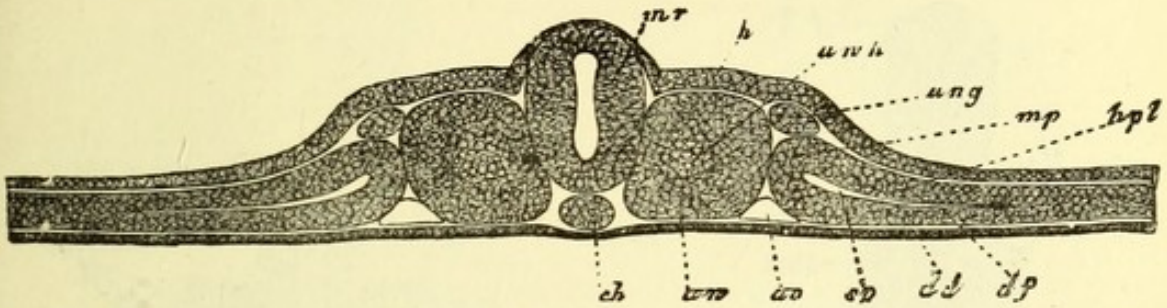


Fig. 279.—Transverse section through the embryo of a chick on the second day where the medullary canal is closed. (Kölliker.)

mr. Medullary canal.
h. Epiblast.
uwh. Cavity of protovertebra *uw*.
ung. Wolffian duct.
mp. Mesoblast dividing.
hpl. Somatopleure.
df. Splanchnopleure.
sp. Pleuroperitoneal cavity.
dd. Hypoblast.
ch. Notochord.

are lost, and take no permanent part in the formation of the embryo.

Beneath the medullary canal the cells of the mesoblast are altered to form a rod-shaped cellular body, which following the line of the canal lies in the axis of the embryo; this is the *chorda dorsalis* or *notochord*.

Supporting the medullary canal on either side of the chorda dorsalis are masses of mesoblast, somewhat quadrangular in section, which are termed the *vertebral plates;* continuous with these externally are other thinner masses of mesoblast called the *lateral plates*.

The lateral plates become divided into an upper part or *somatopleure*, which is in close relationship to the epiblast, and a lower part, the *splanchnopleure*, which is next to the hypoblast; the space between these being the *pleuroperitoneal cavity*. The vertebral plates become separated from the lateral plates by a longitudinal partition, so that on either side of the neural canal is a mass of undivided mesoblast extending laterally towards the divided mesoblast.

In each vertebral plate there appear transverse vertical interruptions at definite intervals which split the plate up into a number of quadrangular blocks of mesoblast, known as the *protovertebræ;* the number of these corresponds to the number of vertebræ of the animal.

These protovertebræ become subdivided by transverse fissures into external parts, the *muscle plates*, which form eventually the dorsal and other muscles, and internal parts which become the permanent vertebræ.

From these inner portions processes of mesoblast grow upwards

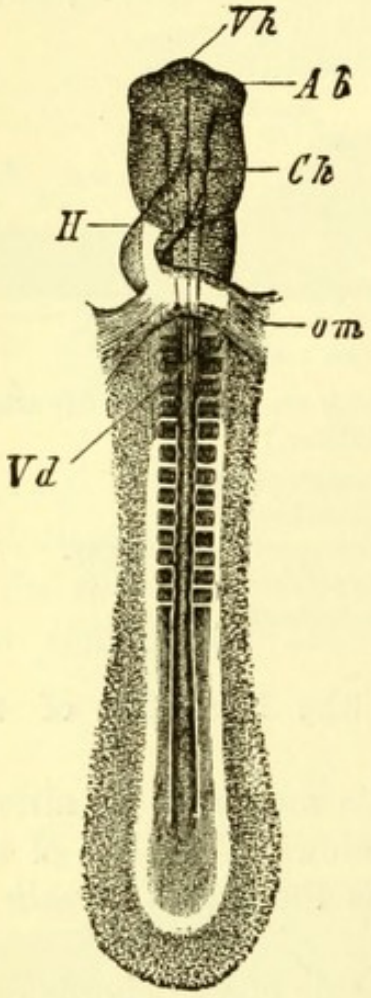


Fig. 280.—Embryo chick at the end of the second day seen from below. (Kölliker.)

Vh. Forebrain.
Ab. Optic vesicles.
Ch. Notochord.
H. Heart.
om. Omphalo-mesenteric veins.
Vd. Lower opening of foregut.

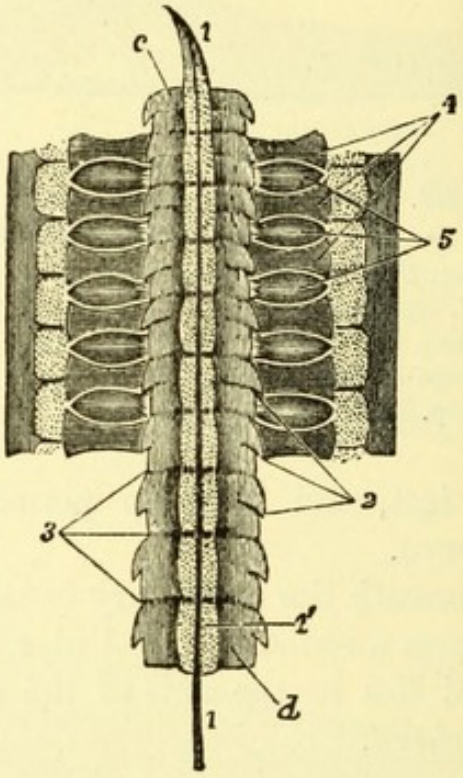


Fig. 281.—Division of the vertebral column of a chick. (Kölliker after Remak.)

1. Notochord.
2. Points of separation of the original protovertebræ.
3. Points of division of the permanent vertebræ.
4. Arches of the vertebræ.
5. Spinal ganglia.

c. Body of first cervical vertebra.
d. One of the lower vertebræ.

over the medullary canal to meet with processes from the protovertebræ of the opposite side. Mesoblastic tissue also grows inwards between the medullary canal and the notochord, and between the notochord and subjacent hypoblast.

These projections beneath the notochord meet with others from

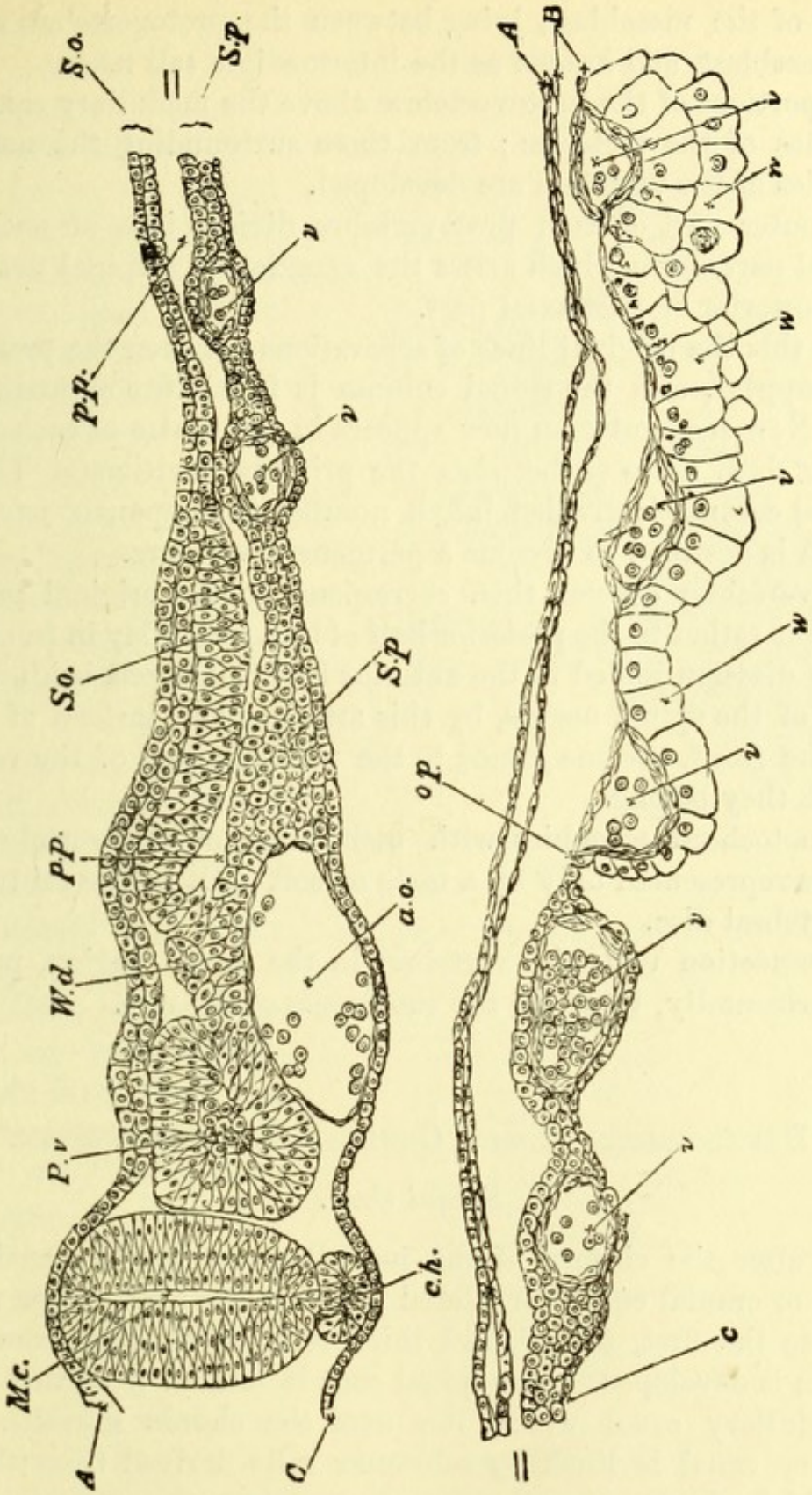


Fig. 282.—Transverse section through the dorsal region of an embryo chick of forty-five hours. (Foster and Balfour.)

A. Epiblast.
M.c. Medullary canal.
P.v. Proto-vertebræ.
W.d. Wolffian duct.
p.p. Pleuroperitoneal cavity.
S.o. Somatopleure.
S.p. Splanchnopleure.
v.v. Vessels.
a.o. Aorta.
B. Mesoblast.
C. Hypoblast.
o.p. Line of union of opaque and pellucid areas.
w. Spheres of the white yolk.

a mass of the mesoblast, lying between the protovertebræ and the cleft mesoblast, and known as the intermediate cell mass.

The portions of the protovertebræ above the medullary canal form the arches of the vertebræ ; from those surrounding the notochord the bodies of the vertebræ are developed.

The outer part of each protovertebra divides into an anterior or pre-axial part, from which arises the ganglion of a spinal nerve, and into a posterior or post-axial part.

After this the original lines of separations between the protovertebræ disappear, and the spinal column is fused into a cartilaginous mass. New segmentation now appears in the centre of each original protovertebra, midway between the primary divisions. Thus the vertebral column is divided into a number of component parts, each of which is destined to become a permanent vertebra.

The vertebræ do not then correspond to the original protovertebræ, but rather to the posterior half of that which lay in front of the primary division joined to the anterior half of the one behind. The ganglia of the spinal nerves, by this arrangement, instead of belonging to the front, become joined to the posterior part of the vertebra, to which they belong.

The notochord atrophies with ossification of the vertebræ, and finally is represented only by a mass of soft cells in the centre of an intervertebral disc.

In connection with the vertebræ in the dorsal region, processes grow horizontally, these are the rudiments of the ribs.

Development of the Central Nervous System.

Spinal Cord.

Soon after the closure of the medullary or neural canal at its anterior or cranial end, it is dilated in this region into three vesicles known as the first, second, and third cerebral vesicles, from which the brain is developed. The spinal cord is formed from that part of the medullary canal which lies over the chorda dorsalis. The medullary canal is lined by columnar cells derived from the epiblast, which, shortly after they are shut off from the general epiblast, develop at the sides of the canal, so as to narrow the lumen of the tube by the increase in thickness of its sides. The upper and lower parts of the canal do not become thickened. The side walls approximate to the centre, decreasing laterally the lumen of the canal, which becomes narrow in the middle with a dilatation

above and below. The lateral walls of the canal, thus approximated, unite in the centre, and convert the medullary canal into two separate tubes, a dorsal and a ventral.

The lower or ventral tube of the divided canal becomes the central canal of the spinal cord, and the columnar cells of the epiblast form a lining of ciliated columnar epithelium.

The epiblast at the lower part of the canal becomes converted into the anterior grey columns, in connection with which arise the anterior roots of the spinal nerves; whilst at the upper part the posterior grey columns are formed in connection with the posterior roots of the spinal nerves and their ganglia.

The white columns are thought by some authors to be derived from the mesoblast surrounding the canal, but by others they are assigned to the epiblast.

The upper or dorsal canal becomes converted into a fissure by the absorption of its roof, and is thus changed into the posterior fissure of the spinal cord.

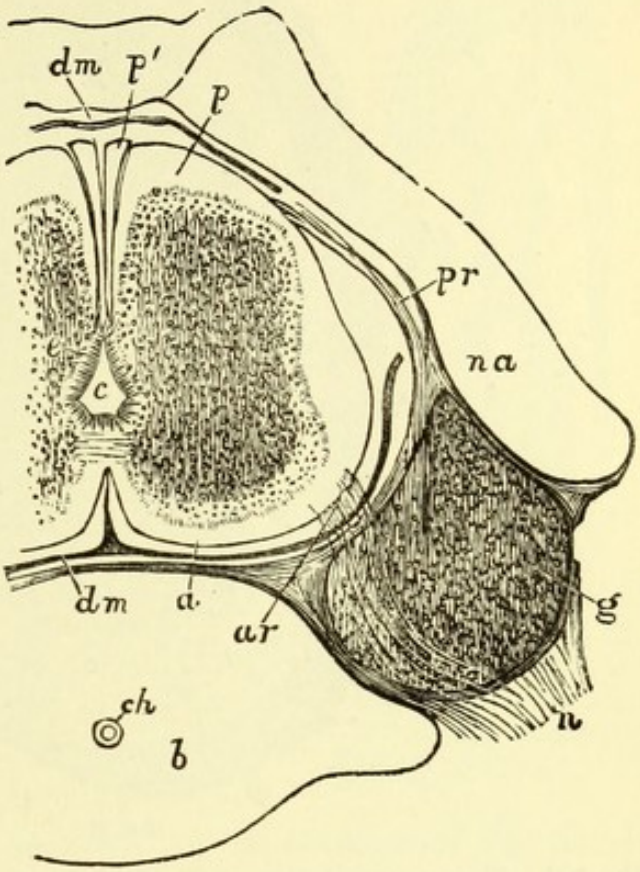


Fig. 283.—Transverse section of the spinal column of the human embryo of from nine to ten weeks. (Kölliker.)

dm. Dura mater.
p'. Columns of Goll.
p. Posterior column.
pr. Posterior root.
na. Arch of vertebra.
g. Ganglion of a spinal nerve.
a. Anterior column.
ar. Anterior root.
ch. Notochord.
b. Body of the vertebra.
n. Spinal nerve.
c. Central canal.
e. Epithelium of canal.

The anterior fissure is formed by the downgrowth of the anterior columns, which diverge, leaving between them an interval which becomes occupied by the pia mater.

The commissures are not formed between the lateral halves of the cord until later. The grey commissure appears first.

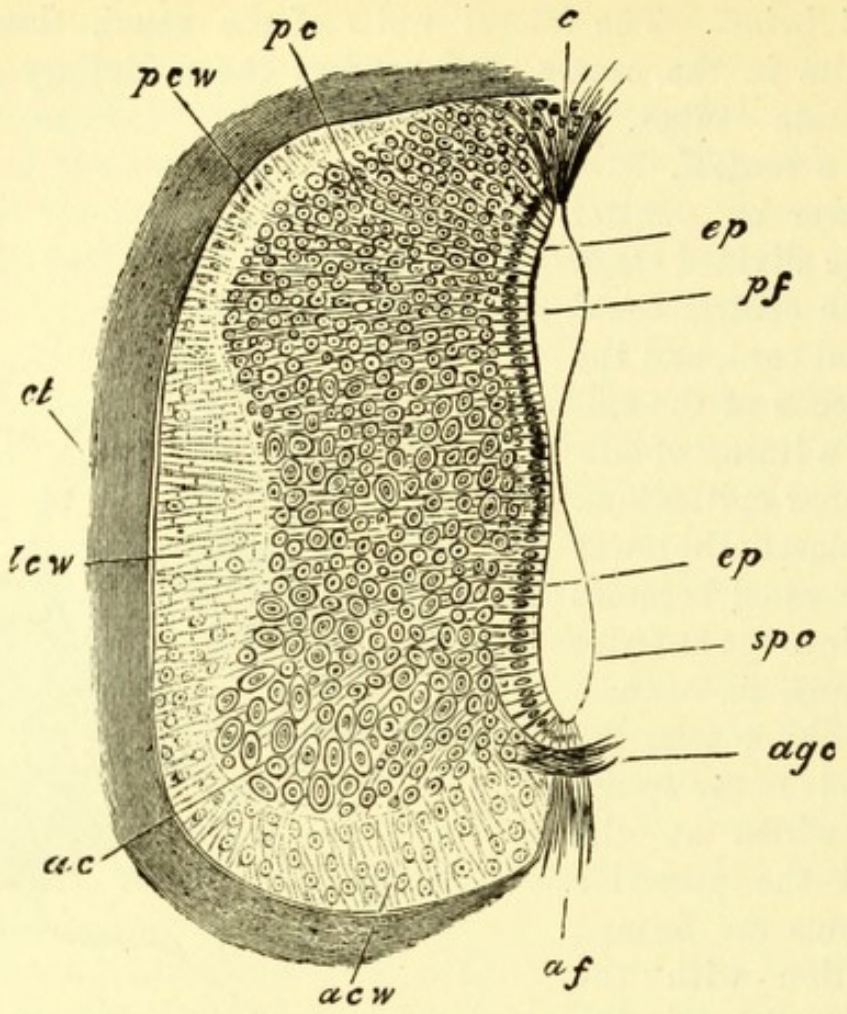


Fig. 284.—Transverse section of the spinal cord of a chick of seven days. (Foster and Balfour.)

ep. Epithelium lining the medullary canal. *pf*. Part of the cavity of the medullary canal which becomes the posterior fissure. *spc*. Permanent medullary tube or central canal of the spinal cord. *agc*. Anterior grey commissure. *af*. Anterior fissure, not yet well formed. *c*. Tissue filling in the upper part of the posterior fissure. *pc*. Cells forming the posterior grey matter. *pcw*. Posterior white column. *ct*. Mesoblast surrounding the spinal cord. *lcw*. Lateral white column. *acw*. Anterior white column. *ac*. Cells forming the anterior grey matter.

The Brain.

Anterior cerebral vesicle.—As already mentioned, the brain is formed from the primitive neural canal, the anterior part of which dilates into three little swellings called the anterior, middle, and posterior cerebral vesicles. From the anterior, or first cerebral vesicle, at an early period spring two processes, which become the optic vesicles. These ultimately develop into the retina, and other nervous parts of the eye, with the history of which the changes occurring in them will be described.

The optic vesicles are pushed downwards by two large processes growing forwards from the anterior vesicle (the primitive cerebral Hemispheres). The anterior part of the brain then appears to be

composed of two divisions, the anterior of which is subsequently developed into the cerebral hemispheres, corpora striata, and the olfactory lobes, as a whole called *prosencephalon*, while the hinder part, representing the anterior vesicle, receives the name of *thalamencephalon*.

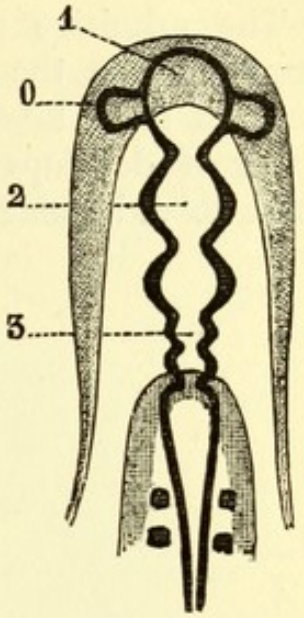


Fig. 285.—Diagram of the cerebral vesicles of the brain of a chick at the second day. (Cadiat.) 1, 2, 3. Cerebral vesicles. 0. Optic vesicles.

The cavity of the thalamencephalon opens behind into the cavity of the middle cerebral vesicle, and in front communicates with the hollow rudiments of the cerebral hemispheres, and eventually it becomes the cavity of the third ventricle. The floor of the thalamencephalon is ultimately developed into the optic chiasma, part of the optic nerves, and the infundibulum. The latter comes in contact with a process from the mouth, uniting with which it ultimately forms the pituitary body. From the posterior part of the roof of the thalamencephalon is developed the pineal gland—a peculiar outgrowth, of unknown function, more elaborately developed in some of the lower vertebrates. The anterior part of the roof of the thalamencephalon becomes very thin, and its place is finally occupied by

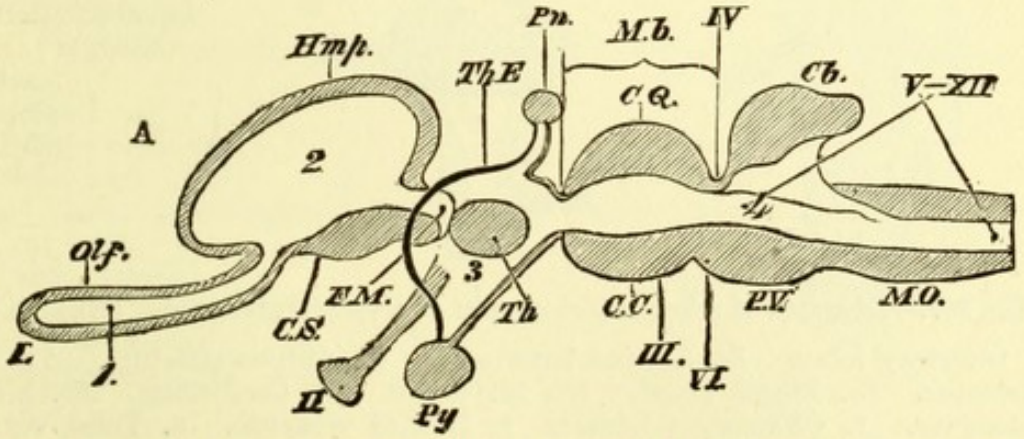


Fig. 286.—Diagram of a vertical longitudinal section of the developing brain of a vertebrate animal, showing the relation of the three cerebral vesicles to the different parts of the adult brain. (Huxley.)

Olf. Olfactory lobes. *Fm.* Foramen of Monro. *Cs.* Corpus striatum. *Th.* Optic thalamus. *Pn.* Pineal gland. *M.b.* Mid brain. *Cb.* Cerebellum. *Mo.* Medulla oblongata. *Hmp.* Cerebral hemispheres. *Th.E.* Thalamencephalon. *Py.* Pituitary body. *CQ.* Corpora Quadrigemina. *C.C.* Crura cerebri. *PV.* Pons Varolii. *I.—XII.* Regions from which spring the cranial nerves. 1. Olfactory ventricle. 2. Lateral ventricle. 3. Third ventricle. 4. Fourth ventricle.

a thin membrane containing a vascular plexus, which persists in the roof of the third ventricle (*choroid plexus*). From the sides of the

thalamencephalon, which become extremely thickened, are developed the *optic thalami.*

The primitive cerebral hemispheres first appear as two lobes growing from the anterior part of the first cerebral vesicle. The floor of these lobes thickens, and forms the *corpora striata,* while the roof develops into the hemispheres proper. The cavities of these lobes become the lateral ventricles, and are connected by the

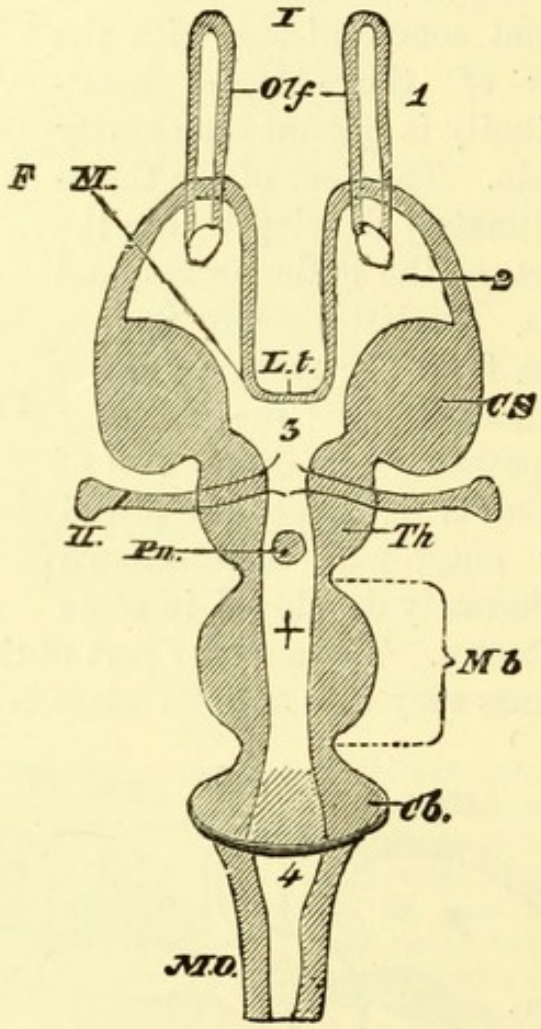


Fig. 287.—Diagram of a horizontal section of a vertebrate brain. (Huxley.)

Olf. Olfactory lobes. *Lt.* Lamina terminalis. *Cs.* Corpus striatum. *Th.* Optic thalamus. *Pn.* Pineal gland. *Mb.* Mid-brain. *Cb.* Cerebellum. *Mo.* Medulla oblongata. 1. Olfactory ventricle. 2. Lateral ventricle. 3. Third ventricle. 4. Fourth ventricle. + Iter a tertio ad quartum ventriculum. *FM.* Foramen of Munro. *II.* Optic nerves.

foramen of Munro, which at the earlier periods is very wide, but subsequently narrows to a mere slit. The cerebral hemispheres are separated at an early stage by a fold of connective tissue, which ultimately forms into the *falx cerebri.* The hemispheres are greatly enlarged in the backward direction, so that they quite overlap the thalamencephalon and the parts developed from the middle cerebral

vesicle. The corpus callosum is subsequently formed by the fusion of the juxtaposed parts of the hemispheres.

From the anterior part of the cerebral hemispheres arise two prolongations, which develop into the olfactory bulbs, these grow forwards, and soon lose their cavities, which at first communicated with those of the ventricles.

Middle cerebral vesicle.—By the cranial flexure the brain is bent at the junction of the first and second cere-

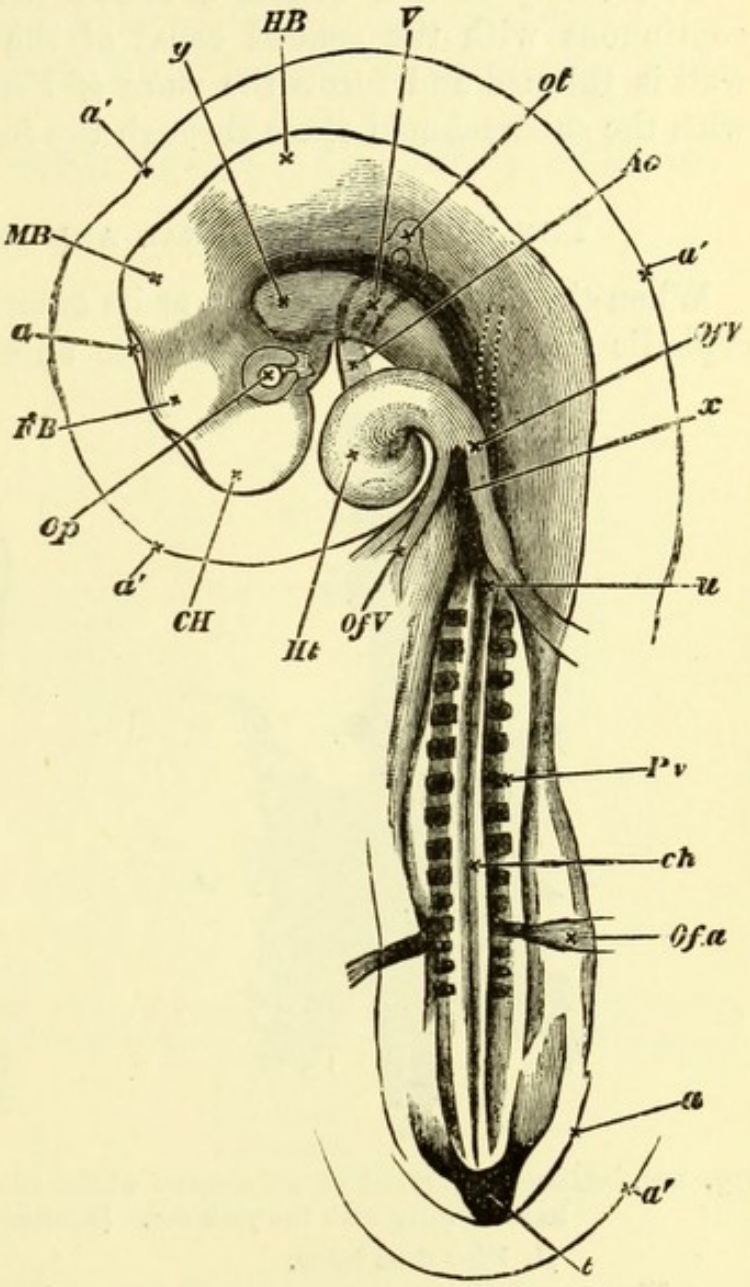


Fig. 288.—Chick on the third day seen from beneath as a transparent object, the head being turned to one side. (Foster and Balfour.)
a'. False amnion.
a. Amnion.
CH. Cerebral hemisphere.
F.B., *M.B.*, *H.B.*, Anterior Middle, and Posterior cerebral vesicles.
op. Optic vesicle.
ot. Auditory vesicle.
ofv. Omphalo-mesenteric veins.
Ht. Heart.
Ao. Bulbus arteriosus.
Ch. Notochord.
Of.a. Omphalo-mesenteric arteries.
Pv. Proto-vertebræ.
x. Point of divergence of the splanchnopleural folds.
y. Termination of the foregut, V.

bral vesicles, the first is thus turned downwards, leaving the second as the most anterior part of the brain.

The upper walls of the middle cerebral vesicle are developed into the corpora quadrigemina.

The cavity of this vesicle persists as a narrow channel, forming a communication between the third ventricle in front, and the fourth ventricle behind, and receives the name in the adult brain of the *iter a tertio ad quartum ventriculum*. The crura cerebri arise from the lower wall of this middle vesicle.

Posterior cerebral vesicle.—This is divided into an anterior and a posterior part. From the roof of the anterior division arises the cerebellum, and from its floor the pons Varolii.

The posterior division gives rise to the medulla oblongata.

The cavity of this vesicle is called the fourth ventricle. It is continuous with the central canal of the spinal cord. Its upper wall is thinned and forms the *valve of Vieussens.* It communicates with the subarachnoid space through the foramen of Majendie.

The Alimentary Canal and its Appendages.

When the blastoderm is bent at its anterior extremity to form the cephalic fold, it closes and forms the anterior boundary of a short

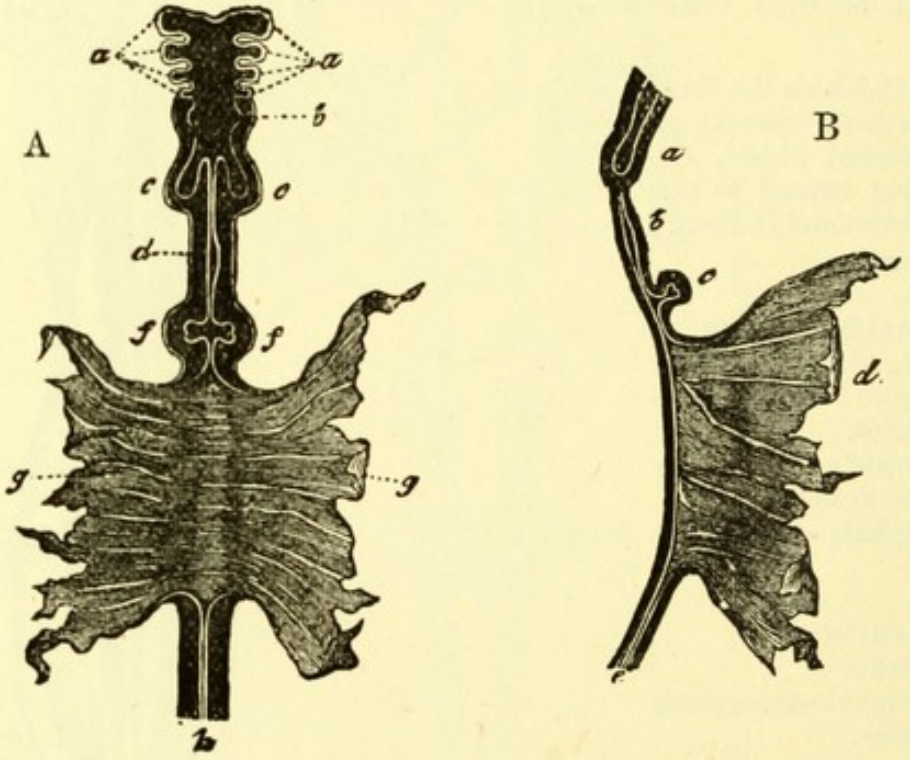


Fig. 289.—Alimentary canal of an embryo whilst the rudimentary mid-gut is still in continuity with the yolk sac. (Kölliker after Bischoff.)

A. View from below.

a. Pharyngeal plates.
b. The pharynx.
c.c. Diverticula forming the lungs.
d. The stomach.
f. Diverticula of the liver.
g. Membrane torn from the yolk-sac.
h. Hind-gut.

B. Longitudinal Section.

a. Diverticulum of a lung.
b. Stomach.
c. Liver.
d. Yolk sac.

canal, the upper wall of which is formed by the general blastoderm, and the lower by that part of the splanchnopleure, which runs backwards, leaving the somatopleure, to form the pleuro-peritoneal space. It then turns forwards to meet the uncleft mesoblast, form-

ing the wall of the yolk sac, which communicates freely with this rudimentary part of the alimentary tract.

This canal becomes closed in for a considerable extent, and is called the *fore-gut*. It is the precursor of the pharynx, the lungs, the œsophagus, the stomach, and the duodenum. The mouth, which at this period is unformed, is developed later by an involution of the epiblast and the removal of the tissue between the fore-gut and the buccal cavity.

The tail fold, in a somewhat similar manner, shuts off a canal

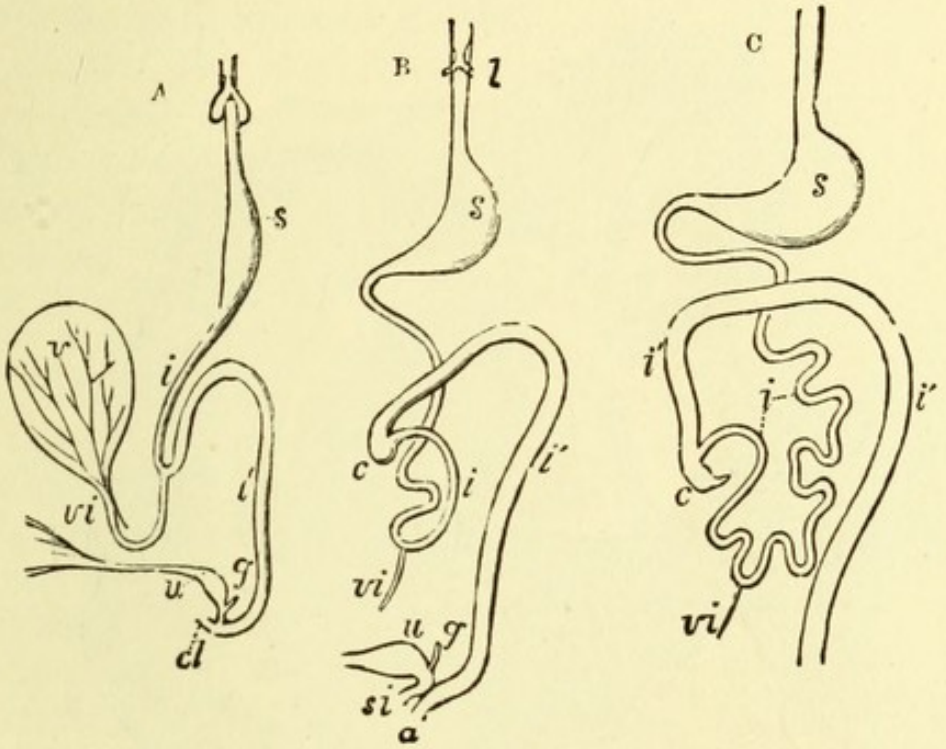


Fig. 290.—Position of the various parts of the alimentary canal at different stages. A. Embryo of five weeks; B. Of eight weeks; C. Of ten weeks. (Allen Thomson.)

l. Pharynx with the lungs.
s. Stomach.
i. Small intestine.
i'. Large intestine.
g. Genital duct.
u. Bladder.
cl. Cloaca.
c. Cæcum.
vi. Ductus vitello-intestinalis.
si. Urogenital sinus.
v. Yolk-sac.

called the *hind-gut*, which becomes developed into the posterior part of the alimentary canal. This hind-gut until the further development of the bladder, &c., is in connection with the allantois which arises as a bud from the lower part of the rudimentary hind-gut.

Between these two canals an intermediate one is formed by the splanchnopleure, which, at a distance from its origin, becomes constricted, and shuts off an upper canal, the *mid-gut*, from the lower larger yolk sac, the connection between the two forming the *ductus vitello-intestinalis*.

Thus the primitive alimentary canal consists of an anterior and a

posterior blind canal, which are closed below, and a third intermediate between these, which opens at its lower surface into the yolk sac.

As the placental circulation becomes more developed, the yolk sac shrinks and atrophies, until it is represented by a fold of tissue connected with the primitive intestine. The ductus vitello-intestinalis accordingly becomes obliterated, and thus the mid-gut is closed at its lower aspect.

The primitive intestine placed at the inferior aspect of the embryo,

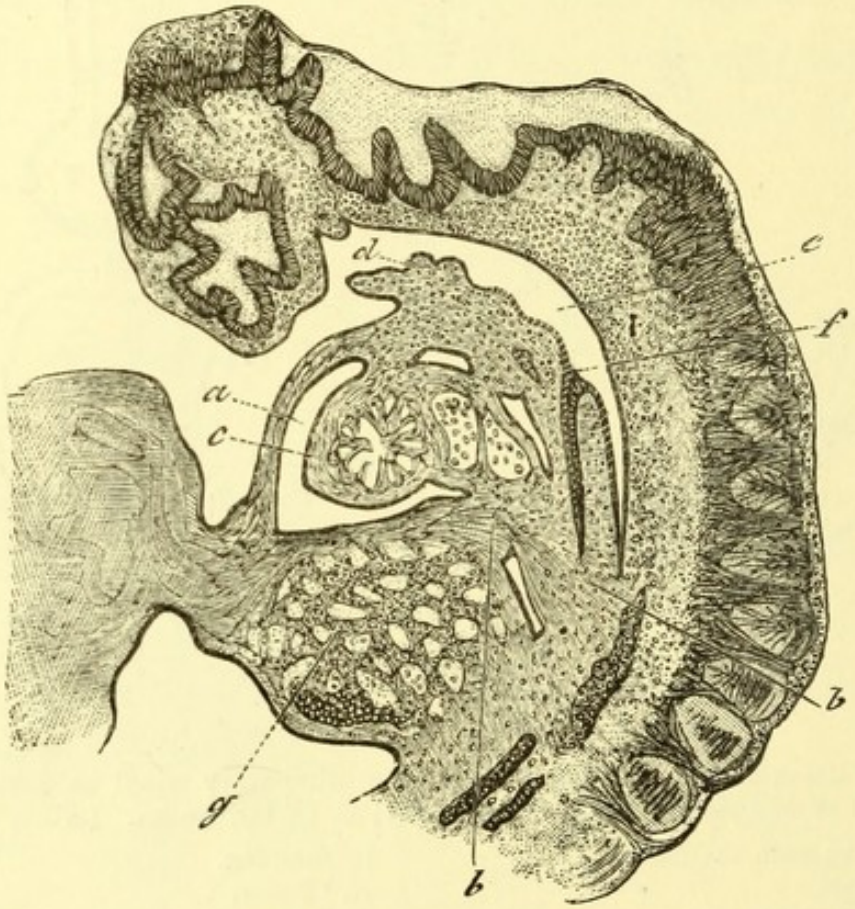


Fig. 291.—Longitudinal section of a fœtal sheep. (Cadiat.)

a. Pericardium.
b. Commencement of Diaphragm.
c. Heart.
d. Branchial arches.
e. Pharynx.
f. Origin of lung.
g. Liver.

just below the protovertebræ, is lined by hypoblast, and covered by mesoblast. The cephalic or anterior extremity of the canal is formed by uncleft mesoblast; the rest of the canal is formed by the splanchnopleural layer.

A dilatation of a part of the fore-gut gives origin to the primitive stomach; this is quite straight at first, lying below the vetebral column, with which it is connected by mesoblast. After a time the stomach becomes turned to the right side, so that the left surface of

the organ lies anteriorly and the right posteriorly, the mesoblast connecting it with the vertebral column, being developed into the peritoneal processes of the organ.

The lower part of the fore-gut is of much smaller calibre than the dilated portion forming the stomach ; it becomes the duodenum, in connection with which arise two important viscera, the liver and the pancreas.

The mid-gut and hind-gut form the small and large intestines, these being at first one straight tube, of which the small intestine has the larger calibre. The small intestine, as it grows, falls into folds, and the mesoblast connecting it to the vertebral column forms the mesentery.

The large intestine is at first a straight tube lying to the left of the embryo; it becomes bent, and part of the tube is directed towards the right side ; this develops another flexure, the portion of intestine below which grows downwards. That part remaining on the left side forms the rectum, the sigmoid flexure, and the descending colon ; whilst that between the flexures becomes the transverse colon, and that on the right side the ascending colon.

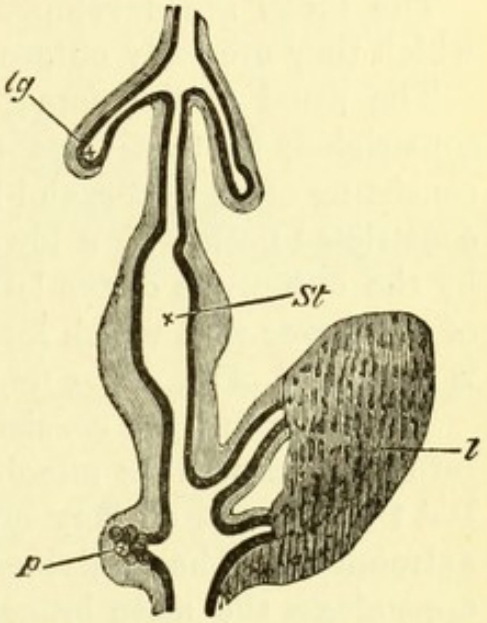


Fig. 292.—Diagram of the alimentary canal of a chick at the fourth day. (Foster and Balfour, after Götte.)

lg. Diverticulum of one lung.
St. Stomach.
l. Liver.
p. Pancreas.

The cæcum is developed from the ascending colon, the ileo-cæcal valve shutting off one part of the intestinal canal from the other. The vermiform appendix originates from the inferior extremity of the cæcum, which, owing to its feeble growth, is of much smaller calibre than the upper part.

The epithelial lining of the intestines is derived from the hypoblast, and the muscular, vascular, connective tissue, and serous coverings are mesoblastic in their origin.

The liver is developed from two diverticula of the duodenum, in connection with which arise cylinders of cells. The hypoblast develops into the liver cells and the cells lining the ducts, the mesoblast furnishing the vascular and connective tissue parts of the organ. The two diverticula are connected by a transverse piece, and form the right and left lobes of the liver.

The process connecting the liver to the duodenum forms the common bile duct, and from this the gall bladder is developed as an outgrowth.

The vessels of the embryo, which are in relation to the liver, will be described under the vascular system.

The pancreas arises as an outgrowth from the duodenum, its constituent parts originating in a manner similar to those of the liver.

The spleen is derived from the mesoblast, and is developed in one of the peritoneal processes of the stomach.

The lungs are developed in connection with the œsophagus, of which they are early outgrowths.

The canal of the fore-gut at a certain point becomes laterally constricted, its transverse section presenting an hour-glass shape. consisting of an upper, and lower dilated portion, united by a central constricted neck. The lower of these cavities becomes sub-divided by the outgrowth of the lateral portions and the upgrowth of a part of the lower wall which forms a central septum, so that the fore-gut is composed of an upper undivided tube, giving off two appendages.

These appendages consist of hypoblastic tissue, and as they grow into the surrounding mesoblast they divide and sub-divide, until at last they consist of very minute tubules, which terminate in dilated extremities. The undivided canal forms the permanent trachea, the appendages the main bronchi, whilst their minute sub-divisions are the bronchioles, which terminate in the dilated alveoli.

The hypoblast forms the delicate lining membrane of the air passages, and the mesoblast gives rise to the supporting tissue holding them together, to the blood-vessels, the muscular, cartilaginous, and connective tissue of the bronchial tubes.

The pleuræ surrounding the lungs are like the other serous membranes mesoblastic in their origin.

Genito-urinary Apparatus.

In the interval between the protovertebræ and the cleavage of the mesoblast into its somatopleural and splanchnopleural layers, a mass of cells arranges itself into a longitudinal ridge. This ridge, which lies beneath the epiblast, becomes hollow, and thus a tube is produced, called the *Wolffian duct*.

From this tube diverticula arise, which extend into the surrounding mesoblast; they are tubular, and communicate with the central duct. The processes become twisted, and at their extremities the

neighbouring mesoblast undergoes differentiation, and forms vascular capsules corresponding in structure to the Malpighian corpuscles. This part of the Wolffian duct, which has acquired a glandular structure, is the *Wolffian body* or primitive kidney of the embryo, whilst the Wolffian duct corresponds to the primitive ureter.

The epithelium lining the interval between the somatopleure and splanchnopleure (pleuroperitoneal cavity) becomes columnar in character close to their origin from the uncleft mesoblast. It receives the name of the *germinal epithelium*. An involution of this takes

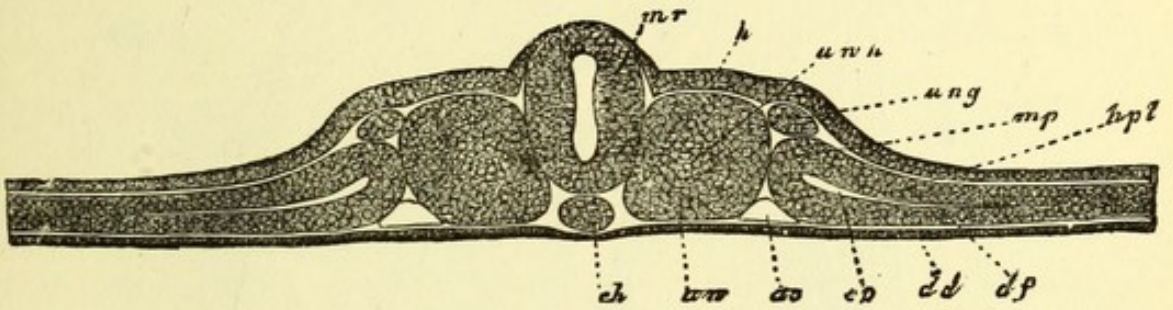


Fig. 293.—Transverse section through the embryo of a chick on the second day where the medullary canal is closed. (Kölliker.)

mr. Medullary canal.
h. Epiblast.
uwh. Cavity of protovertebra *uw*.
ung. Wolffian duct.
mp. Mezoblast dividing.
hpl. Somatopleure.
df. Splanchnopleure.
sp. Pleuroperitoneal cavity.
dd. Hypoblast.
ch. Notochord.

place into the mesoblast, just below the somatopleure, and becomes shut off, forming a hollow cylinder.

By this means a second duct is formed in close relation to the first; this is the *Müllerian duct*. This duct is developed from before backwards.

According as the embryo is a male or a female, so one or other of these ducts develops. In the male the Wolffian duct remains as the vas deferens, and the Müllerian duct becomes atrophied. In the female, on the other hand, the Müllerian duct forms the organs for the conveyance of the ova out of the body, and the Wolffian duct is represented by a rudimentary structure near the ovary.

Part, however, of the Wolffian duct in both sexes develops similarly: this, the *metanephros*, corresponds to that part of the duct nearest to the tail end of the embryo. It forms part of the urinary organs, and develops into the permanent ureter and the kidney.

From the metanephros a projection arises, which grows quickly and opens into the cloaca; this remains as the ureter. From the upper part of the ureter arise small cæcal evolutions, which become convo-

luted at certain points and surrounded by mesoblast; these canals are the urinary tubules, and at the extremity of each is developed a tuft of vessels, which thus forms a Malpighian corpuscle.

The straight tubes group themselves together at the inner part of

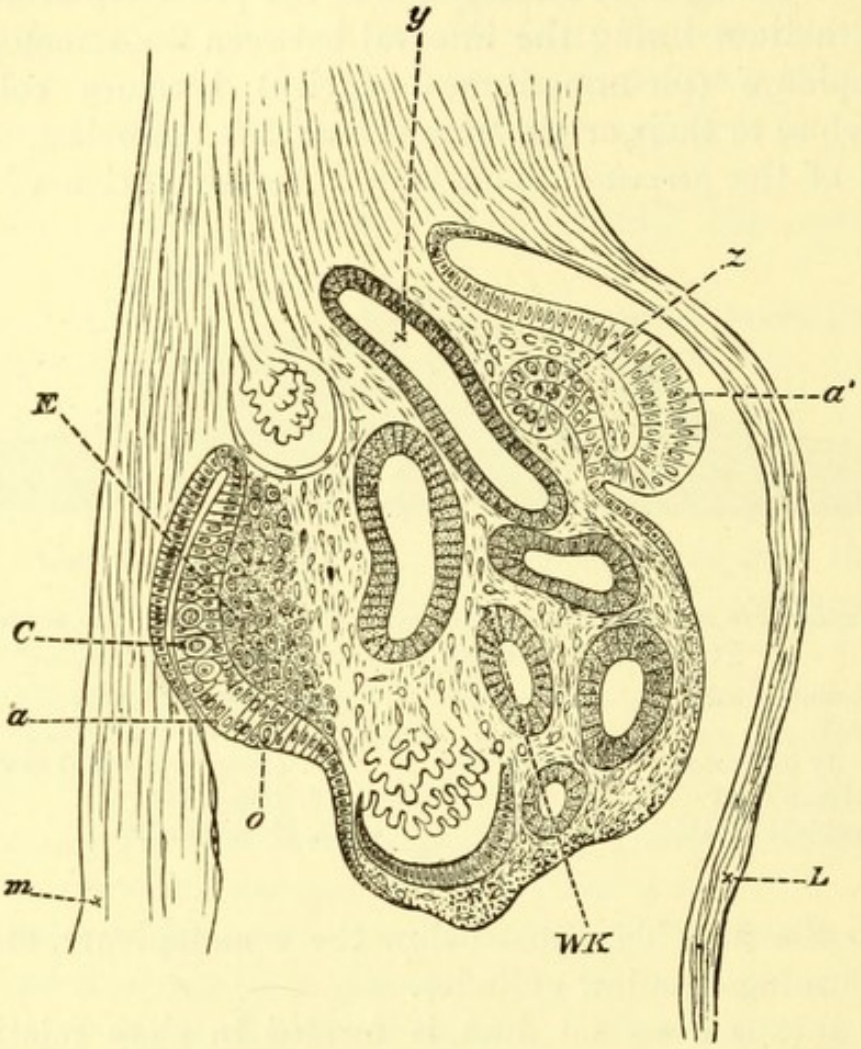


Fig. 294.—Section of the inner part of the pleuroperitoneal cavity through the origin of the genito-urinary organs. (Waldeyer.)

L. Somatopleure.
m. Splanchnopleure.
a. Germinal epithelium.
C, *o*. Primitive ova.
E. Mesoblast forming the ovary.
WK. Wolffian body.
y. Wolffian duct.
a'. Epithelium giving rise to the duct of Müller *z*.

the gland, whilst the convoluted tubules, with the Malpighian corpuscles, are aggregated at the periphery of the gland.

At the junction of the ureter to the glandular mass, changes take place by which this tube is split up into several sub-divisions, which are the primitive calices of the kidney, the dilated part of the ureter forming the pelvis.

The testicle arises partly from the germinal epithelium lining the inner extremity of the pleuro-peritoneal cavity, lying close to the

splanchnopleure, and partly from the mesoblast surrounding the Wolffian body.

The germinal epithelium, the cells of which are not so well developed

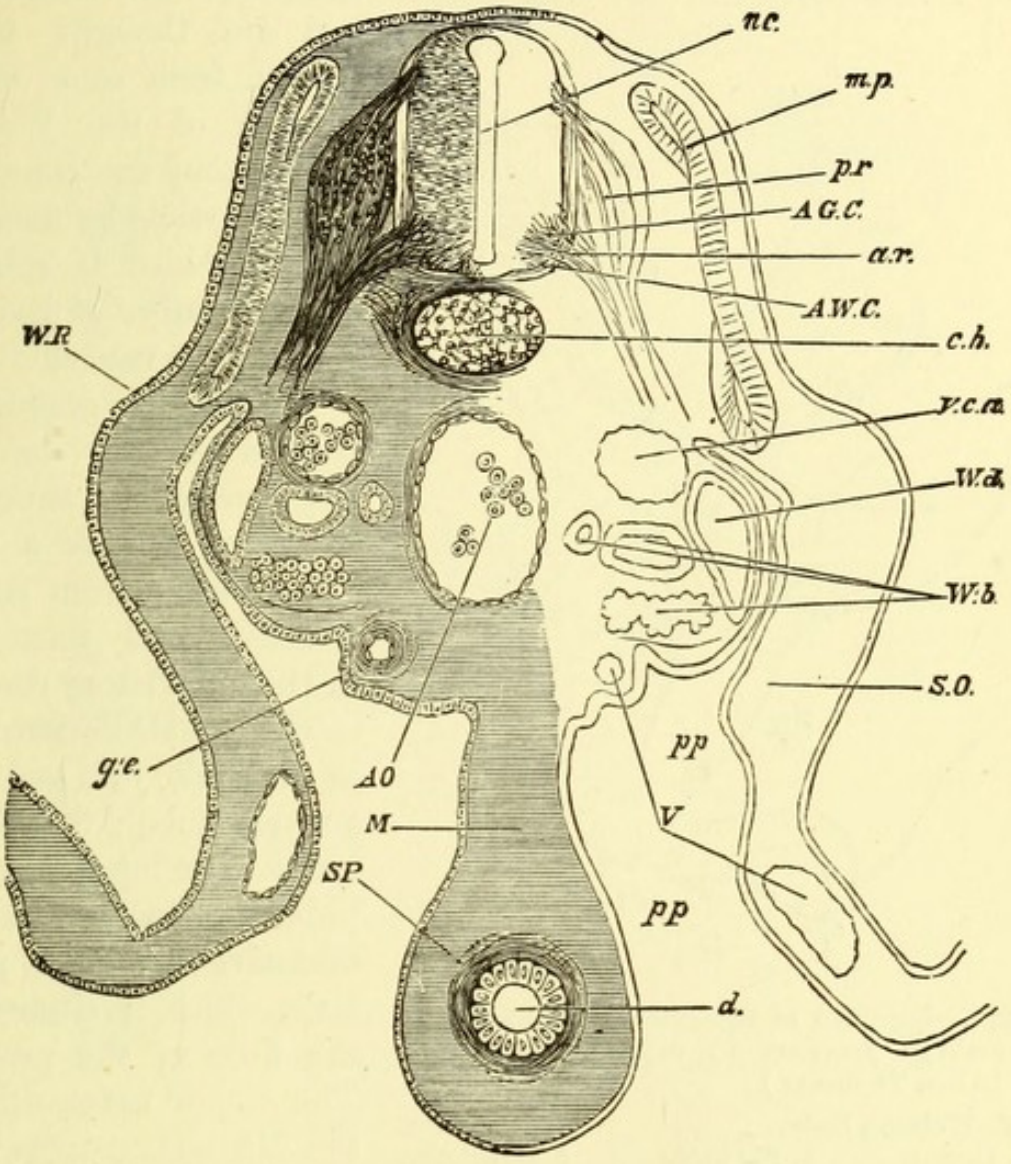


Fig. 295.—Transverse section through the lumbar region of an embryo chick at the end of the fourth day. (Foster and Balfour.)

W.R. Wolffian ridge.
g.e. Germinal epithelium.
A.O. Dorsal aorta.
M. Mesentery.
SP. Splanchnopleure.
d. Alimentary canal.
V. Vessels.
m.p. Commencing Müllerian duct.
So. Somatopleure.
W.b. Wolffian body.
W.d. Wolffian duct.
V.c.a. Posterior cardinal vein.
c.h. Notochord.
A.W.C. Anterior white column of spinal cord.
a.r. Anterior root.
A.G.C. Anterior grey column.
p.r. Posterior root.
m.p. Muscle plate.
nc. Canal of spinal cord.

as in the female, sends processes into the mesoblast, and these are said to form the spermatic cells, the mesoblast becoming differentiated around them to form the walls of the tubuli seminiferi.

The Wolffian duct, which persists as the vas deferens, aids in forming the testicle, the epididymis being merely a convoluted part of it, and the vas aberrans one of the cæcal tubes in connection with the duct. The coni vasculosi are thought to be formed from some of the tubules of the Wolffian body; they are connected to the testicle by means of a tube which is split up into a number of divisions forming the vasa efferentia.

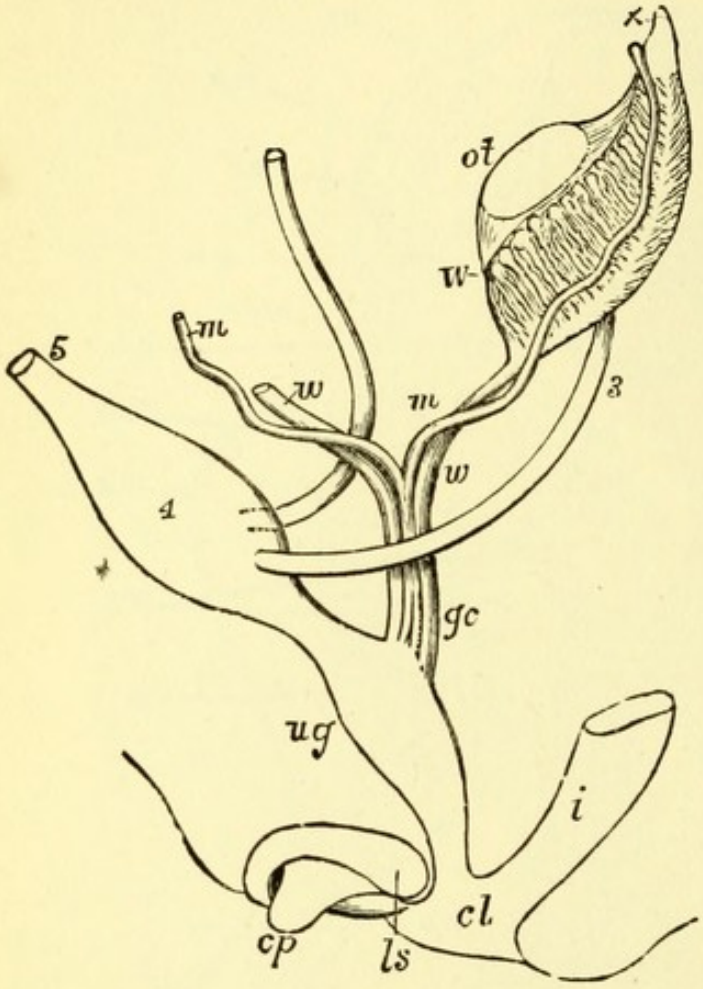


Fig. 296.—Diagram of the genital organs of an embryo previous to sexual distinction. (Allen Thomson.)

W. Wolffian body.
3. Ureter. 4. Bladder. 5. Urachus.
gc. Genital cord. *cp*. Clitoris, or penis.
m. Müllerian duct. *i*. Intestine.
w. Wolffian duct. *cl*. Cloaca.
ug. Urogenital sinus.
ls. Part from which the scrotum or the labia majora are developed.
ot. Origin of the ovary or testicle respectively.
x. Part of Wolffian body subsequently developed into the coni vasculosi.

The two Müllerian ducts, in the male, join and form a single tube; this is not further developed, but atrophies, leaving as its representative the sinus pocularis, which is situated in the floor of the prostate. The upper extremities of the Müllerian ducts form the hydatids of Morgagni.

The ovary, like the testicle, is formed from the germinal epithelium, which multiplies and forms a projection close to the Wolffian body. The cells of the epithelium become involuted and surrounded by the uncleft mesoblast, to form ova and Graafian follicles. The glandular part of the ovary thus arises from the germinal epithelium, and its stroma springs from the mesoblast in the neighbourhood of the Wolffian body.

The ducts of Müller are the precursors of the female genital

passages. They approach one another and unite along a certain distance at their lower extremities. Of this united part, the upper end forms the uterus, and the lower the vagina, whilst the un-united parts of the Müllerian ducts form the Fallopian tubes, which

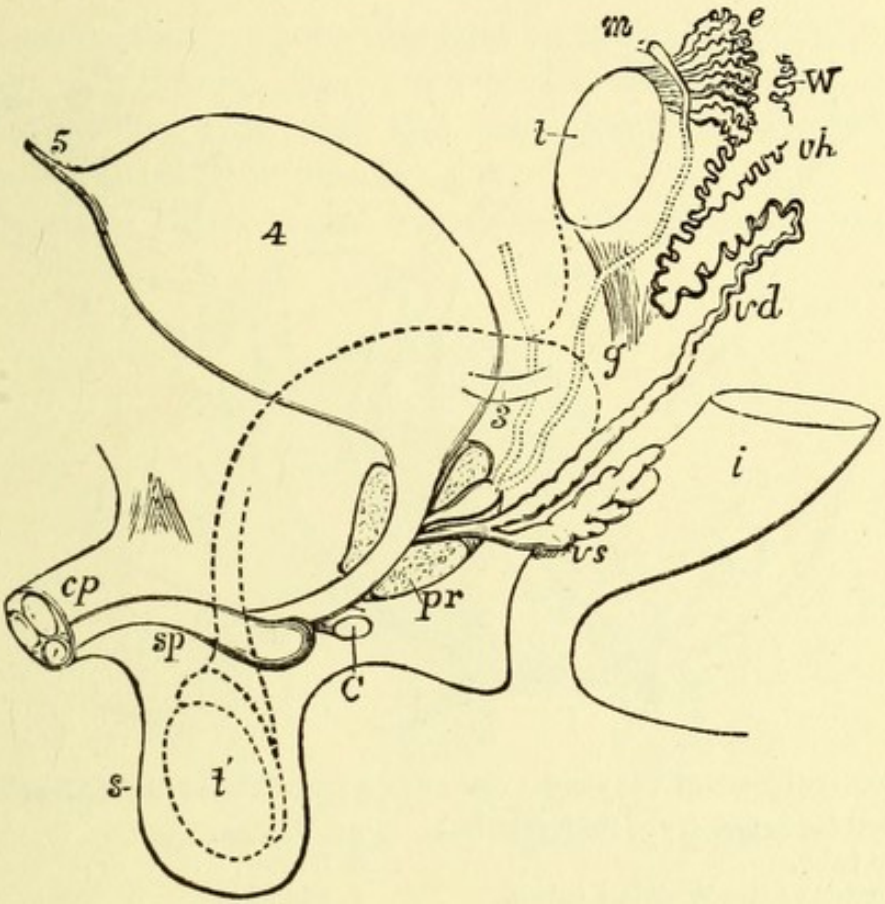


Fig. 297.—Diagram of the sexual organs of the male embryo. (Allen Thomson.)

3. Ureter.
4. Bladder.
5. Urachus.
t. Testicle.
m. Atrophied duct of Müller (hydatid of Morgagni.)
e. Epididymis.
g. Gubernaculum testis.
vs. Vesicula seminalis.
i. Intestine.
pr. Prostate.
W. Organ of Giraldès.
vh. Vas aberrans.
vd. Vas deferens.
C. Cowper's gland.
cp. Penis.
sp. Spongy part of the Urethra.
t'. Position the testicle ultimately assumes.
s. Scrotum.

become connected with the ovaries, whilst their cavities remain continuous with the pleuroperitoneal space.

In the female the Wolffian duct and body atrophy, the parovarium being in the adult the representative of the Wolffian body.

The bladder is merely a dilated portion of that part of the allantois which is in immediate connection with the alimentary canal, and the urachus is the narrowed part of the allantois connecting the bladder to the remainder of the allantois which is without the body walls of the fœtus.

While the alimentary canal is in connection with the allantois, the intestinal and genito-urinary passages open into a common cavity at their termination ; this is the *cloaca*, and it is in the further development of the embryo that a septum arises, dividing this into an alimentary or anal portion, and an anterior or urinary portion. The

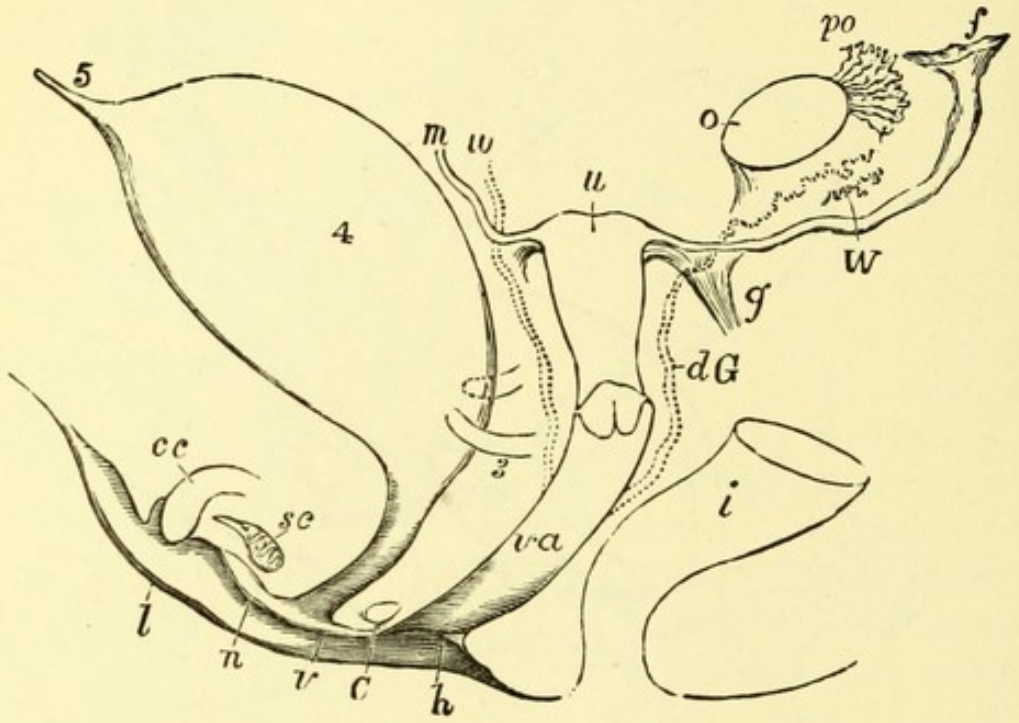


Fig. 298.—Diagram of the sexual organs of a female embryo. (Allen Thomson.)

f. Fimbriated extremity of the left Fallopian tube.
W. Remains of the Wolffian tubes.
g. Round ligaments.
o. Ovary.
po. Parovarium.
u. Uterus.
dG. Remains of Wolffian duct, or duct of Gaertner.
m. Right Fallopian tube cut short.
w. Right obliterated Wolffian duct.
va. Vagina.
3. Ureter.
4. Bladder.
5. Urachus.
h. Inferior opening of vagina.
C. Gland of Bartholin.
v. Vulva.
sc. Vascular bulb.
cc. Clitoris.
n. Nympha.
l. Labium. *i*. Rectum.

septum, dividing the urogenitary from the alimentary portion of the cloaca, forms, externally, the perinæum.

At the aperture of the cloaca an eminence arises which develops into the penis in the male, the clitoris in the female. Around this eminence is a fold of integuments, which forms the labia in the female, the scrotum in the male.

In the female this integumentary covering enlarges much more than the clitoris and covers it in, the urethral orifice opening just below the clitoris.

In the male the urethral orifice at first opens at the base of the

penis, but eventually a groove is formed on the under surface of this organ, which becomes converted into a canal, and forms the urethra.

Blood-Vascular System.

In the mammalian embryo this may be appropriately divided into two systems of different dates ; the first, or early circulation, which is confined to the yolk sac ; and the second, or later circulation, which passes through the placenta.

The Primitive Heart arises from the splanchnopleural layer of

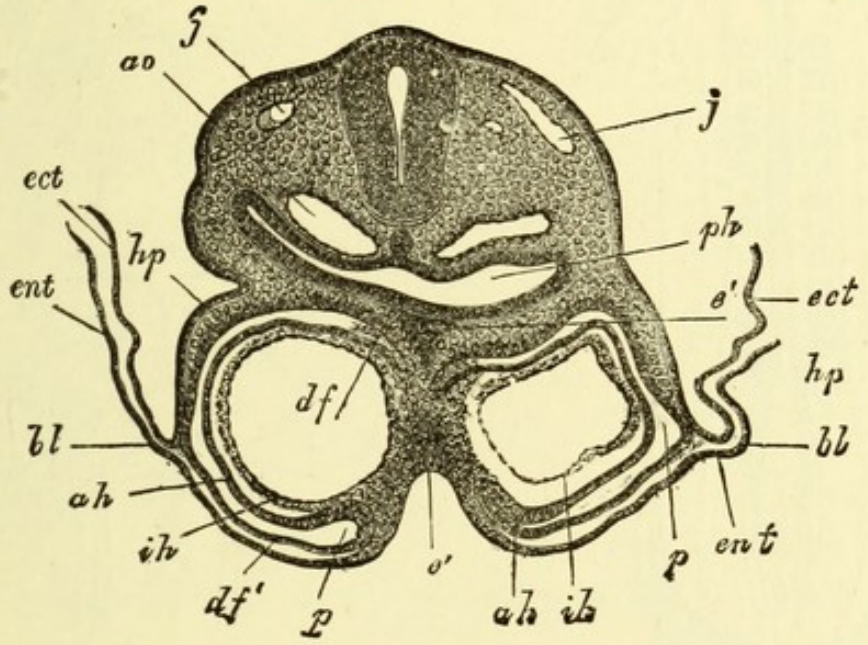


Fig. 299.—Transverse section through the region of the heart of a rabbit's embryo of nine days old. (Kölliker.)

jj. Jugular veins.
ao. Aorta.
ph. Fore-gut.
bl. Blastoderm.
hp. Body wall reflected in *ect*.
ent. Hypoblast.
e'. Prolongation of hypoblast between the two halves of the heart.
ah. Outer wall of the heart.
p. Cavity of the pericardium.
ih. Inner lining of the heart.
ect. Epiblast.
df. Visceral mesoblast.

the mesoblast, just at the point where this forms the under wall of the fore part of the alimentary canal. When the formation of the folds of the embryo was described, it was stated that the groove of the cephalic fold tended to grow backwards towards the tail end of the embryo. This groove is limited behind by the somato-pleural layer of the mesoblast, and posteriorly to this is a cavity formed by the cleavage of the mesoblast, called the pleuroperitoneal cavity. In the early stages of development, the posterior wall of this small cavity is formed by the splanchnopleural layer of the

mesoblast. The heart arises at the point at which the splanchnopleure tends to travel forwards to meet the uncleft mesoblast, and thus completes the pleuroperitoneal cavity.

The heart consists at first of a single cylinder, which in the human embryo is probably formed by the coalescence of two primary tubes.

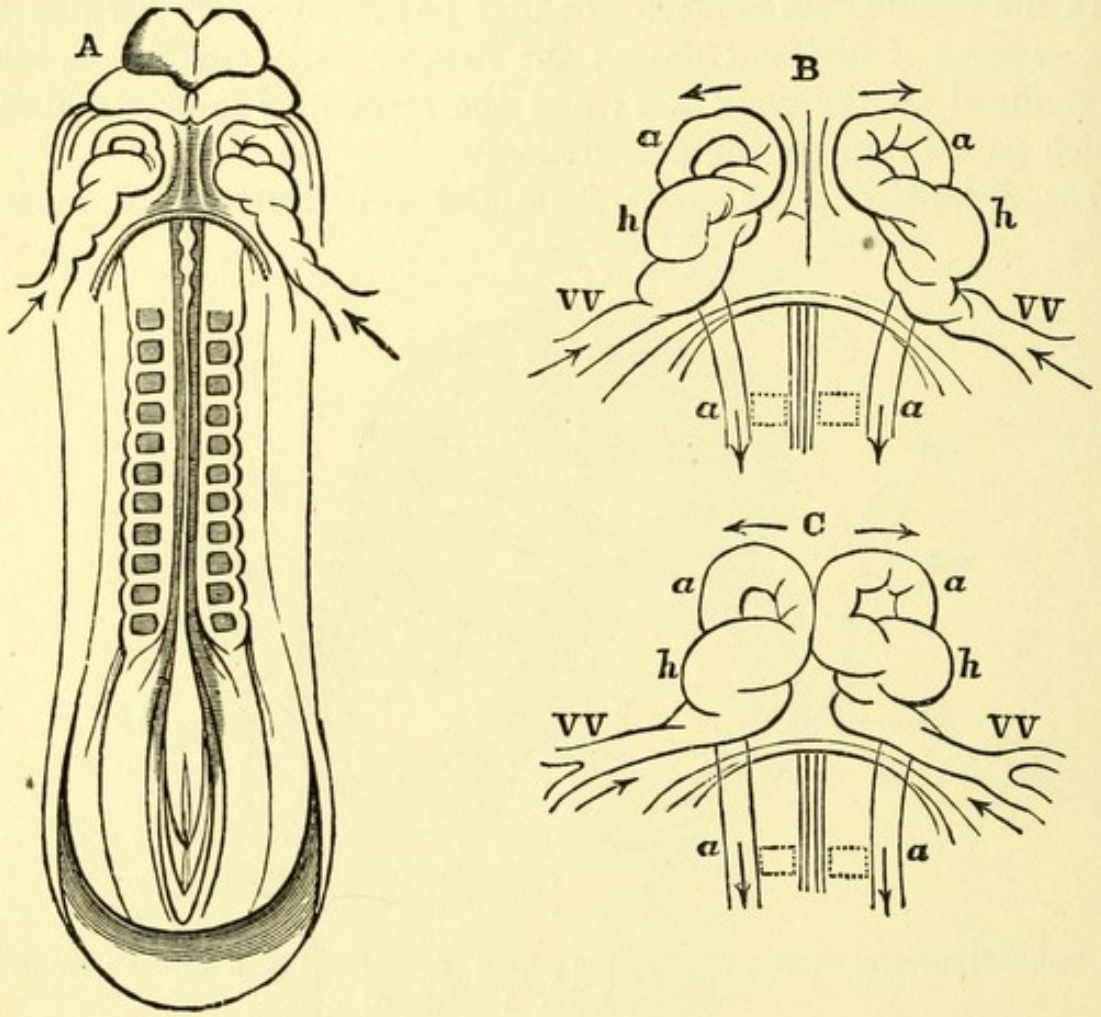


Fig. 300.—Diagrammatic views of the under surface of an embryo rabbit of nine days and three hours old, showing the development of the heart. (Allen Thomson.)

A, View of entire embryo. P, an enlarged outline of the heart of A. C, a later stage of the development of B. *hh*. Ununited heart. *aa*. Aortæ. *VV*. Vitelline veins.

At first it has no distinct cavity, but soon the cells of the mesoblast within the mass forming the heart become transformed into blood corpuscles, and thus it is hollowed out. A layer of endothelial cells line the cavity, and become the endocardium.

The primitive heart is connected at its upper end with the two aortæ, and at its lower end with the omphalo-mesenteric veins.

After a time the tube shows signs of division into three parts; the upper part becomes the aortic bulb, next to which is formed the cavity of the ventricle, continuous with which is the auricular space. The tube also, which at first lies in a straight line, now becomes

twisted on itself, the auricular part becoming posterior and superior, whilst the ventricle, with the aortic bulb, remains anterior and somewhat below.

Each primitive cavity of the heart is divided into two by the gradual growth of partitions, and thus the four permanent heart cavities are developed.

Externally a notch shows the division of the ventricle into right

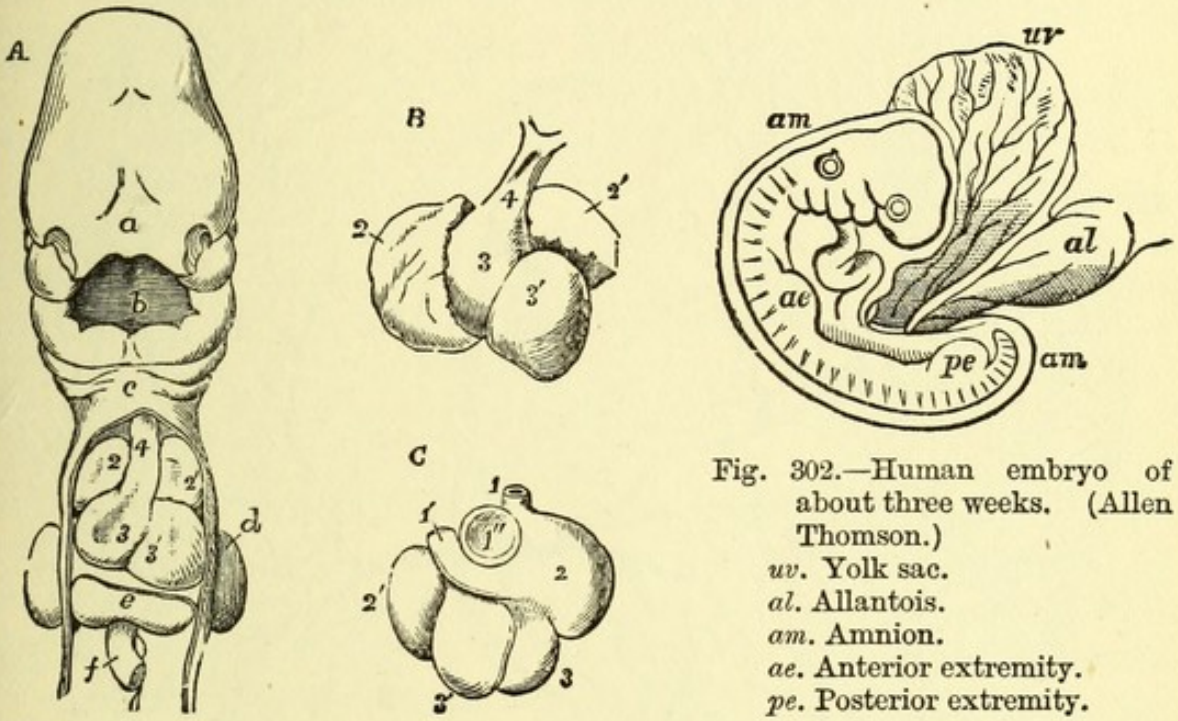


Fig. 302.—Human embryo of about three weeks. (Allen Thomson.)
uv. Yolk sac.
al. Allantois.
am. Amnion.
ae. Anterior extremity.
pe. Posterior extremity.

Fig. 301.—Development of the heart in the human embryo, from the fourth to the sixth week.

A. Embryo of four weeks. (Kölliker after Coste.)

B. Anterior, and C. posterior views of the heart of an embryo of six weeks. (Kölliker after Ecker.)

a. Upper limit of buccal cavity. *c*. Buccal cavity. *b*. Lies between the ventral ends of the 2d and 3rd branchial arches. *d*. Buds of upper limbs. *e*. Liver. *f*. Intestine. 1. Superior vena cava. 1′. Left superior vena cava or connection between the left brachio-cephalic vein and the coronary vein. 1″. Opening of inferior vena cava. 2. 2′. Right and left auricles. 3. 3′. Right and left ventricles. 4. Aortic bulb.

and left cavities, whilst from the inside of the right wall there grows a projection which sub-divides the ventricle internally. This septum is, however, not at once complete at its upper part, a communication between the right and left sides of the heart remaining for some time above this partition. With the growth of the inter-ventricular septum, the external notch becomes less prominent, but is permanently recognisable as the inter-ventricular groove.

In the auricles a fold develops from the anterior wall, which

ultimately unites with a process of later development from the posterior wall. This septum is not complete during fœtal life, but

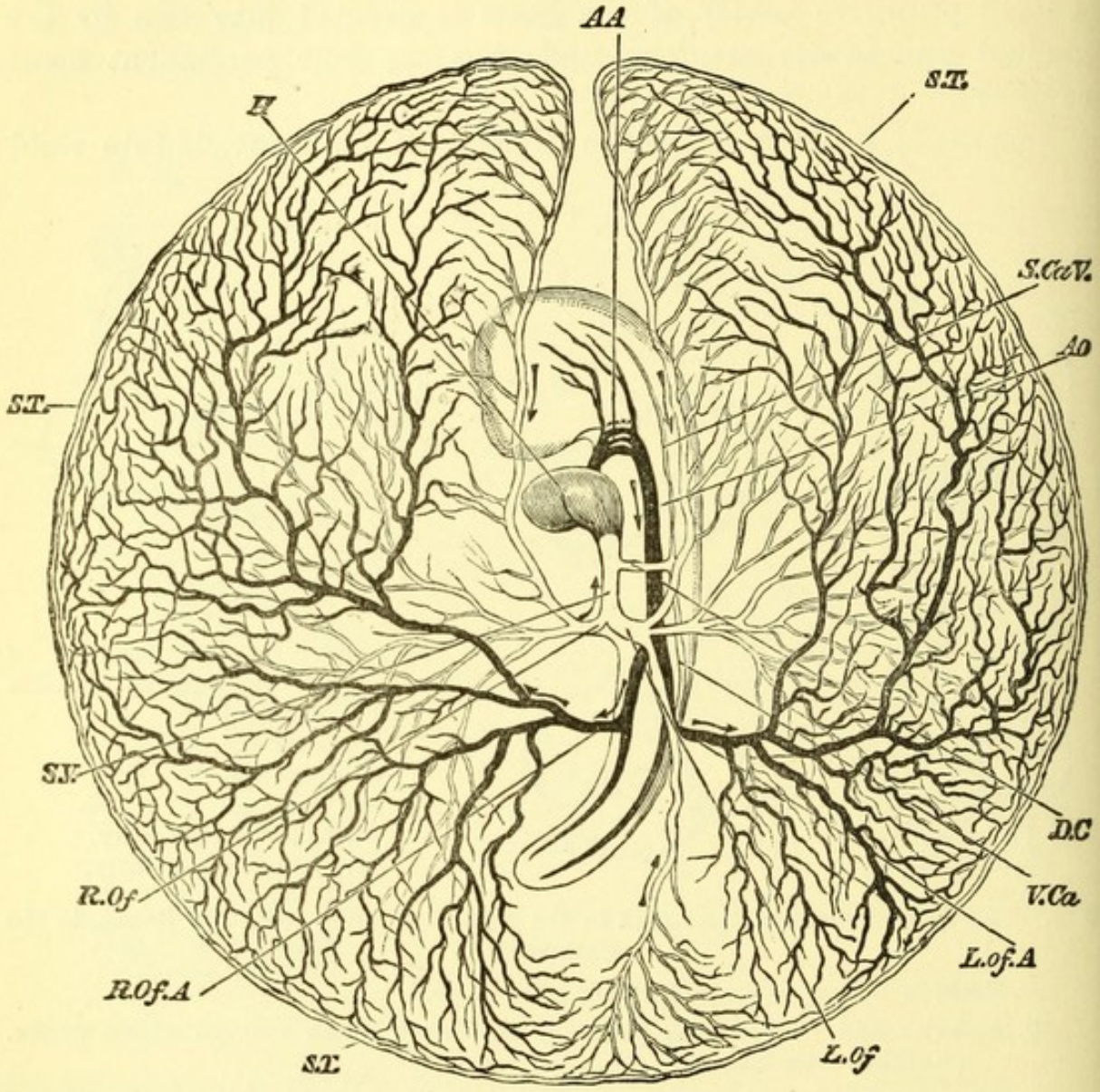


Fig. 303.—Diagram of the circulation of a chick at the end of the third day. (Foster and Balfour.)

H. Heart.
AA. Aortic arches (2nd, 3rd, and 4th).
Ao. Dorsal aorta.
L.of.A., *R.of.A.* Right and left omphalo-mesenteric arteries.
S.T. Sinus terminalis.
R.of., *and L.of.* Right and left omphalo-mesenteric veins.
S.V. Sinus venosus.
D.C. Duct of Cuvier.
S.Ca. and V.Ca. Superior and inferior cardinal veins.

is interrupted by an opening leading from one auricle to the other, called the foramen ovale.

Simultaneously with the appearance of the posterior process of the septum, another fold arises, which is placed at the mouth of the inferior vena cava, and forms the Eustachian valve.

The aortic bulb likewise, by a projection from the inner wall of

the cavity, becomes divided into two canals, the anterior of which remains in continuity with the right ventricle, while the posterior is continuous with the left ventricle. The anterior thus becomes the pulmonary artery, and the posterior the permanent aorta.

The primitive circulations of a human embryo may be divided into two, which differ in their time of appearance and in the accessory organs to which they are distributed. Though they may, for the sake of clearness, be described as two independent circulations, they are not strictly so, as they exist for a short time coincidently, and arise in connection with one another from the same heart.

(*a*) The *earlier or vitelline circulation* is that which is directed to the yolk sac, the embryo obtaining nourishment from the vitellus or yolk; this is an organ of quite secondary importance in the mammalian embryo, and hence this circulation may be better studied in some such animal as the chick, which depends, throughout its embryonic life, on the vitellus for nourishment. In the human embryo the vitelline circulation is chiefly of importance for the few days immediately preceding the development of the placental circulation.

The aortic bulb is continuous with two vessels which run on either side of the primitive pharynx; these are the aortæ, and from each of them a large branch is given off. These omphalo-mesenteric arteries pass to the yolk sac, and there become split up into a number of small vessels, the blood from them being returned partly by corresponding omphalo-mesenteric veins, partly by a large vein running round the periphery of the vascular area known as the *sinus terminalis*. The sinus terminalis opens partly into the right and partly into the left omphalo-mesenteric veins, which subsequently unite into a common venous trunk, called the sinus venosus, which is continuous with the primitive auricle.

This vitelline circulation in the human embryo persists but a short time. After the fifth or sixth week of fœtal life it becomes obliterated, the yolk then being atrophied, and the placental circulation well developed.

(*b*) The *later*, or *placental circulation*, is developed in the mesoblastic layer of the allantois, especially in that part which is in relation with the decidua serotina. The allantois, when fully developed, extends to the chorion, over which it spreads, sending in processes to occupy the villi. These chorionic villi are embedded in the decidua of the uterus, and are especially developed at the upper part, which is in connection with the decidua serotina or maternal placenta.

The primitive aortæ, which were at first two separate tubes,

become united in the dorsal region of the embryo, so that the two aortic arches end in a single vessel, which extends to the middle of the embryo, and there divides into two branches, each of which gives off a vessel called the vitelline or omphalo-mesenteric artery.

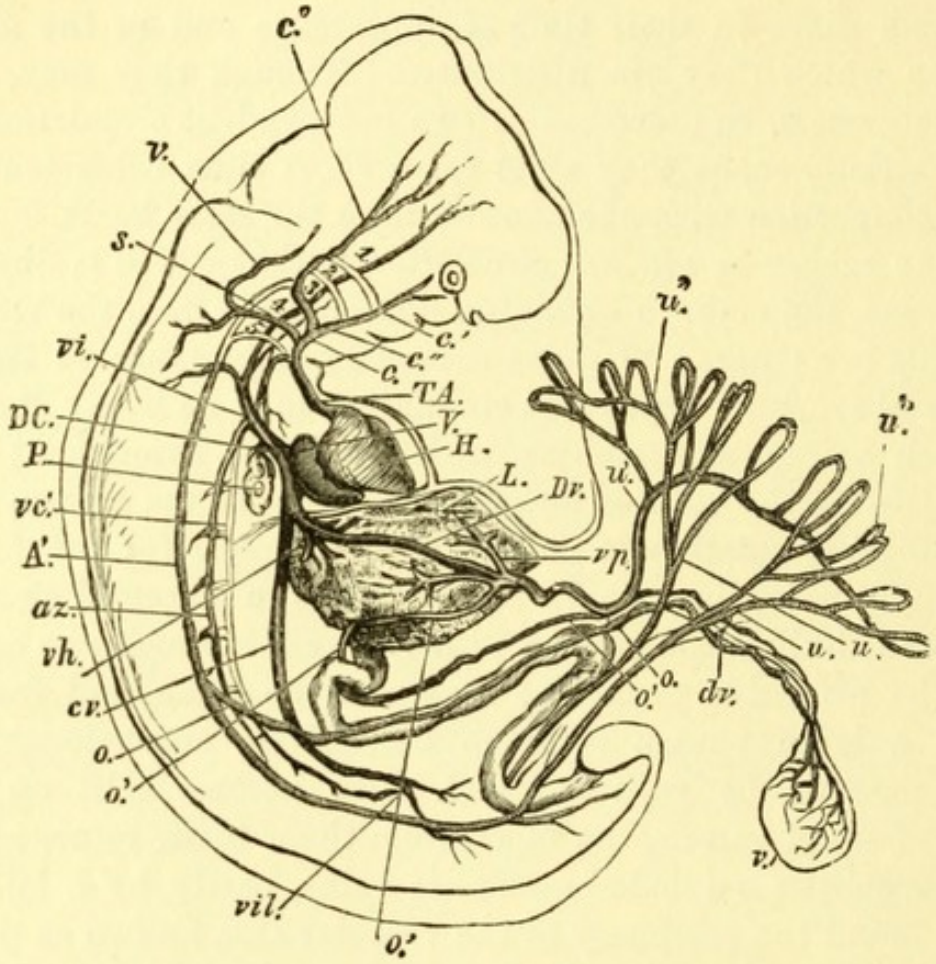


Fig. 304.—Diagram of the vascular system of a human fœtus. (Huxley.)

H. Heart.
T.A. Aortic trunk.
c. Common carotid artery.
c'. External carotid artery.
c''. Internal carotid artery.
s. Subclavian artery.
v. Vertebral artery.
1, 2, 3, 4, 5, Aortic arches.
A'. Dorsal aorta.
1. Omphalo-mesenteric artery.
dv. Vitelline duct.
o'. Omphalo-mesenteric vein.
v'. Umbilical vesicle.
vp. Portal vein.
L. Liver.
uu. Umbilical arteries.
u'' u''. Their endings in the placenta.
u'. Umbilical vein.
Dv. Ductus venosus.
vh. Hepatic vein.
cv. Inferior vena cava.
vil. Iliac veins.
az. Vena azygos.
vc. Posterior cardinal vein.
DC. Duct of Cuvier.
P. Lungs.

From the branches of the aortæ arise two large vessels, which, running along the allantois, spread out over the chorion, being especially directed to the upper part of this membrane; these are the umbilical or hypogastric arteries, which carry the blood from the aortæ to the fœtal placenta.

Veins arise from the terminal networks of these arteries, and combine to form the two umbilical veins. The umbilical veins take a similar course to the arteries, and convey the blood to the venous trunk formed by the junction of the omphalo-mesenteric veins.

After a time the right umbilical and right omphalo-mesenteric veins disappear, whilst from the trunk formed by the junction of the left umbilical and left omphalo-mesenteric veins, branches are given

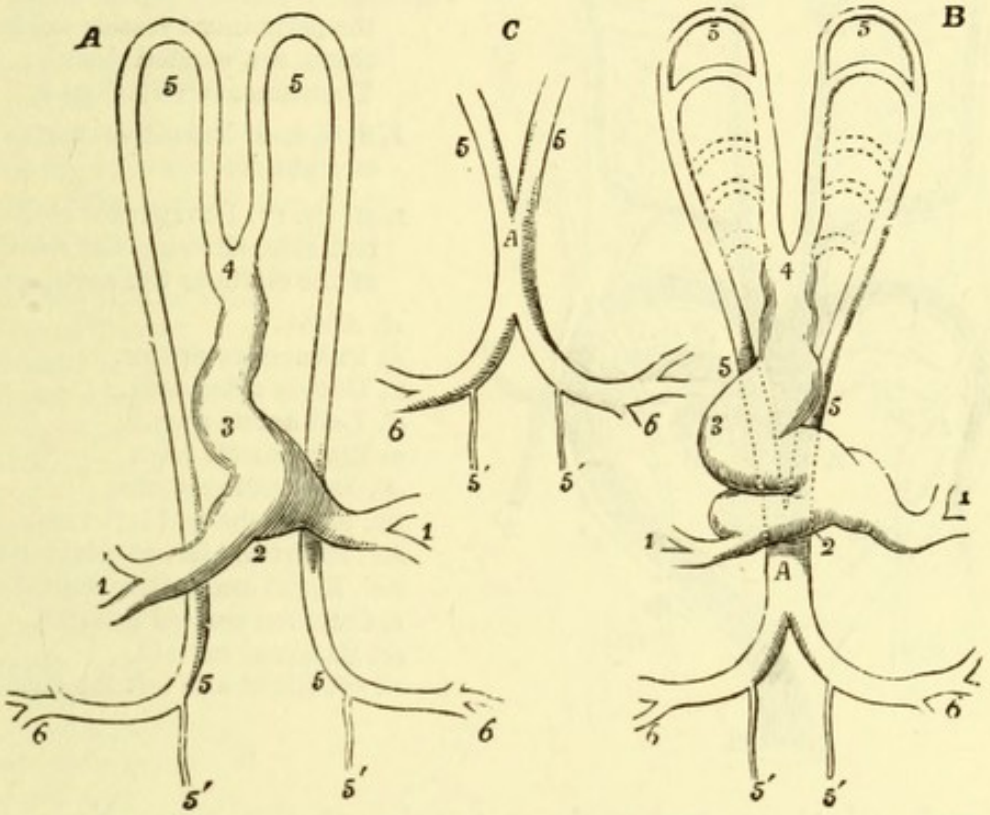


Fig. 305.—Diagram of the heart and principal arteries of the chick. (Allen Thomson.)
B. and C. are later than A.

1, 1. Omphalo-mesenteric veins.
2. Auricle.
3. Ventricle.
A. United Aorta.
4. Aortic bulb.
5, 5. Primitive aortæ.
6, 6. Omphalo-mesenteric arteries.

off to the liver (*venæ advehentes*), and at a point nearer the heart, vessels are received from the liver (*venæ revehentes*).

To the part of the vessel intervening between the origin of the venæ advehentes and the entrance of the venæ revehentes is given the name of the *ductus venosus*.

Thus it may be seen that in the placental circulation the blood is conveyed from the aorta, by the umbilical arteries, to the fœtal placenta, undergoes changes, owing to its close relationship to the maternal blood. From the placenta it is returned by the umbilical vein, which sends a part through the liver and a part direct to the heart. The more minute details of fœtal circulation will be described later on.

The Arterial System.—Around the pharynx are developed five pairs of aortic arches. These commence anteriorly from the two primitive aortæ, and, passing along the side of the pharynx, end in the aortæ as they descend to become united in the dorsal region of the embryo. The points of origin of the arches are termed their anterior roots, and the points of termination their posterior roots.

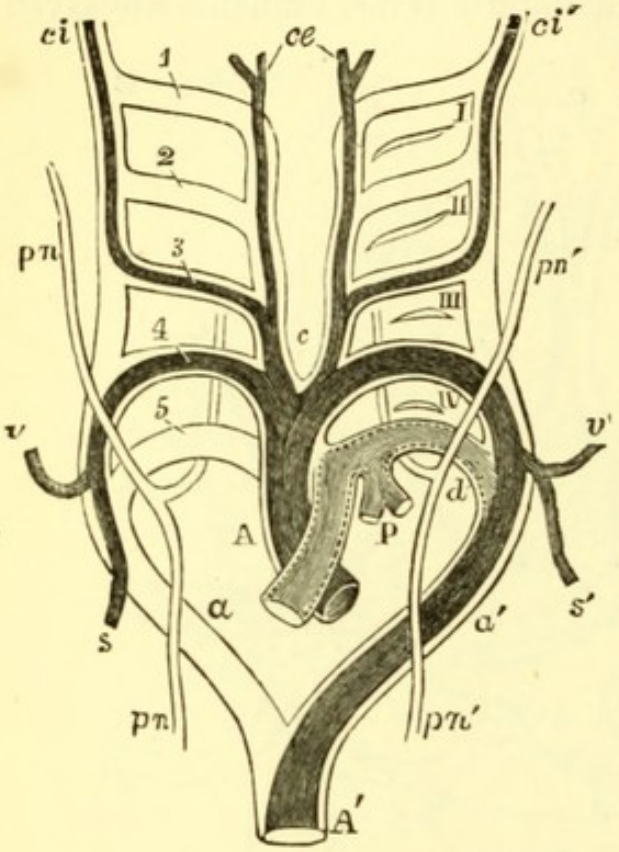


Fig. 306.—Diagram of the aortic arches, the permanent vessels arising from them are shaded darkly. (Allen Thomson after Rathke.)

1, 2, 3, 4, 5, Primitive aortic arches of right side.

I. II. III. IV. Pharyngeal clefts of the left side, showing the relationship of the clefts to the aortic arches.

A. Aorta.
P. Pulmonary artery.
d. Ductus arteriosus.
a'. Left aortic root.
a. Right aortic root.
A'. Descending aorta.
pn. *pn'*. Right and left vagi.
s.s'. Right and left subclavian arteries.
v.v'. Right and left vertebral arteries.
c. Common cartoid arteries.
ce. External cartoid.
ci. *ci'*. Right and left internal carotid.

Though all these arches do not exist at the same time, still, in describing the vessels which arise from them, they may be conveniently considered together.

On the right side the fifth arch disappears completely. On the left side the anterior root and neighbouring part of the fifth arch are transformed into the pulmonary artery; the remaining part of this arch continues as the *ductus arteriosus*, which connects the pulmonary artery with the permanent aorta.

The fourth left arch, in mammalia, becomes the permanent aorta. At the junction of the fourth and fifth left posterior roots the left subclavian artery is given off. In birds the right fourth arch is transformed into the permanent aorta; and in examining the development of the aortic arch of the chick, it must be borne in mind that it is on the opposite side to that it occupies in man.

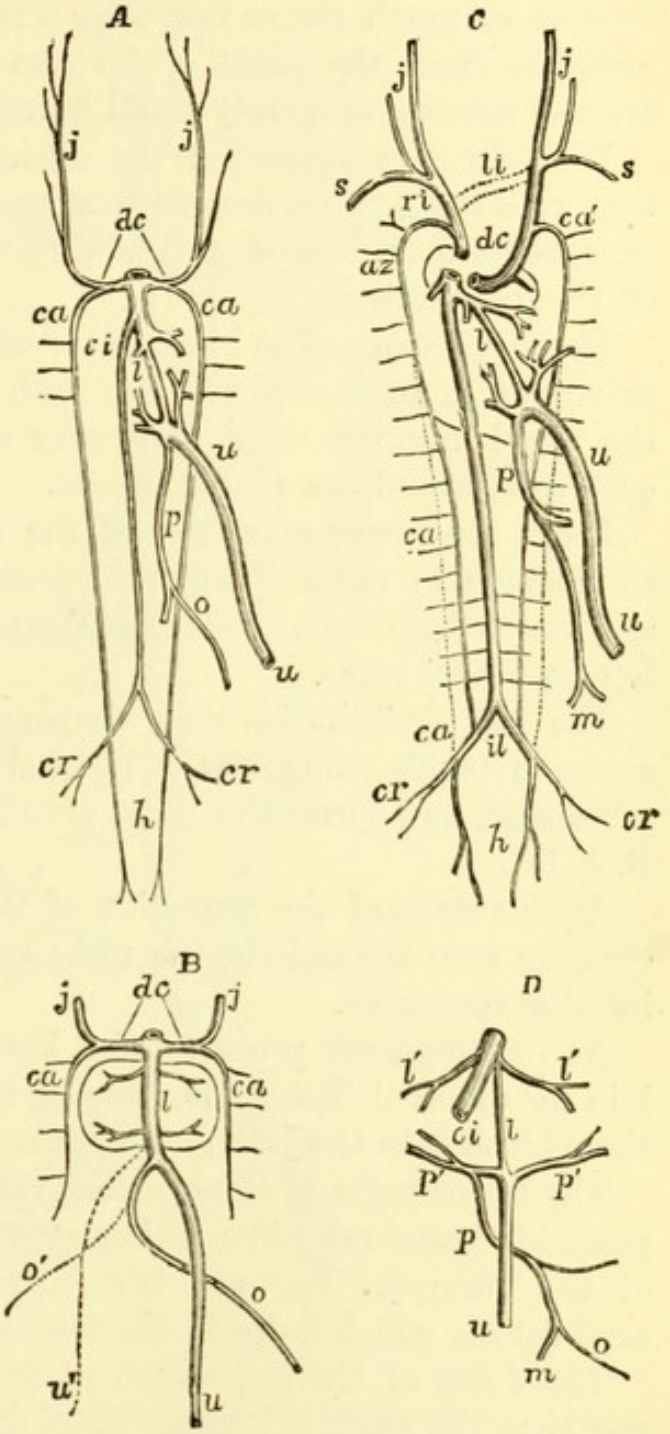
On the right side the anterior root of the fourth arch, and the part of the aortic trunk leading to it, persist as the innominate artery, the fourth arch being represented by the right subclavian artery.

The part of the primitive aortic trunk joining the fourth and third right anterior roots becomes the common carotid artery of the same side, whilst arising from this is the internal carotid, which, taking the

Fig. 307.

A. Plan of principal veins of the fœtus of about four weeks old.
B. Veins of the liver at an earlier period.
C. Veins after the establishment of the placental circulation.
D. Veins of the liver at the same period.

j. Primitive jugular veins.
dc. Ducts of Cuvier.
ca. Cardinal veins.
ci. Inferior vena cava.
l. Ductus venosus.
u. Umbilical vein.
p. Portal vein.
o. Vitelline vein.
cr. External iliac veins.
o'. Right vitelline vein.
u'. Right umbilical vein.
l'. Hepatic veins (venæ revehentes).
p' p'. Venæ advehentes.
m. Mesenteric veins.
az. Azygos vein.
ca'. Remains of left cardinal vein.
li. Cross branch from left jugular which becomes the left brachio-cephalic vein.
ri. Right innominate vein.
s.s. Subclavian veins.
h. Hypogastric veins.
il. Division of inferior vena cava into the common iliac veins.



position of the third arch, passes to the posterior roots, and occupies the trunk of the primitive aorta from the third to the first arches.

The external carotid, arising from the common carotid at the third anterior root, occupies the position of the vessel joining this root to those of the second and first arch.

On the left side the common carotid and its branches are developed

similarly to those on the right, the only difference being that the common carotid arises from the aorta and not from the innominate.

The iliac arteries are developed from the hypogastric. At first they appear as branches, but with the growth of the limbs they become so much larger that after birth they appear to be the main branches from the point of division of the aorta, the hypogastric arteries now being merely small branches of the iliac vessels.

With the development of the organs and limbs, vessels in connection with those above described arise in the mesoblast. It is, however, beyond the scope of this work to describe in detail the origin of the lesser vessels.

Venous System.—The blood is returned from the head by the two primitive jugulars, which unite with the cardinal veins conveying the blood from the trunk and lower extremities to form a vessel on each side, called the *duct of Cuvier*.

From the lower extremity of the embryo the inferior vena cava commences by the union of the external iliac veins; this passes up and opens into the venous trunk common to the left vitelline and left umbilical veins.

The left vitelline becomes continuous with the vessels from the common trunk going to the right side of the liver (the right vena advehens), and forms the main trunk of the portal vein (Fig. 307, B. & D.).

At this stage of the formation of the veins there are three trunks opening into the auricle, the right and left ducts of Cuvier and the inferior vena cava.

As development proceeds, the lower parts of the cardinal veins join the external iliac veins, forming the common iliacs, and so return their blood into the inferior vena cava.

The upper parts of the cardinal veins become continuous with the posterior vertebral veins which convey the blood from the parietes of the embryo. Between the latter a communicating branch is established, which helps in the formation of the azygos zein.

The ducts of Cuvier, which at first were placed almost at right angles to the auricle, become more oblique in their direction as the heart descends.

Between the primitive jugular veins a cross branch is developed. which conveys the blood from the left side of the head and upper extremity of the duct of Cuvier of the opposite side.

The left duct of Cuvier, below the communicating branch, atrophies and forms part of the coronary veins of the heart. The connection between this and the vein above the cross branch being, in the adult,

represented by a small vein, or a band of fibrous tissue, called the vestigial fold of the pericardium.

The cross branch from the left to the right jugular becomes the left innominate vein. The right duct of Cuvier and the right jugular,

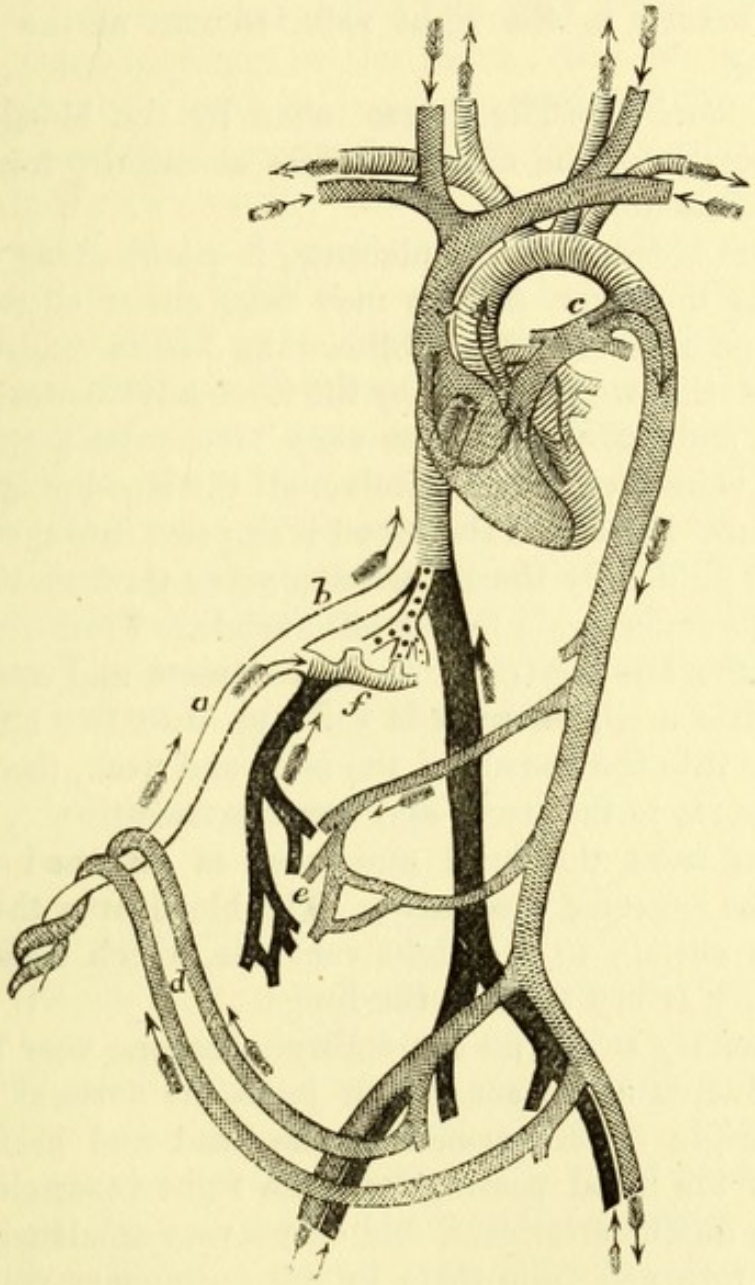


Fig. 308.—Diagram illustrating the circulation through the heart and the principal vessels of a fœtus. (Cleland.)

a. Umbilical vein.
b. Ductus venosus.
f. Portal vein.
e. Vessels to the viscera.
d. Hypogastric arteries.
c. Ductus arteriosus.

below the entrance of this cross branch, form the superior vena cava; whilst the part of the right primitive jugular immediately above the entry of the left innominate vein, forms the right innominate vein.

The posterior vertebral vein of the right side forms the vena azygos major; the corresponding branch of the opposite side, together with the part of the left primitive jugular below the cross branch, forms the left superior intercostal vein and the superior vena azygos minor. The lower part of the left posterior vertebral vein, together with the connecting branch to the right vein, remain as the inferior vena azygos minor.

Fœtal Circulation:—The course taken by the blood through the heart and vessels of the embryo differs essentially from that which persists in adult life.

Tracing the blood from the placenta, it passes along the umbilical vein towards the liver, here it may take either of two courses to reach the vena cava, one which follows the ductus venosus and avoids the liver, the other which passes by the venæ advehentes (portal veins) to the liver, and proceeds by the vena revehentes (hepatic veins) to the inferior vena cava, which receives all the blood passing by both of these channels. From this the blood is emptied into the right auricle, and hence is guided by the Eustachian valve through the septum by the patent foramen ovale to the left auricle. From the left auricle it passes to the left ventricle, which contracts and sends the blood into the aortic arch, where it is split up into two streams, one of which passes into the vessels of the head and neck, the other by the descending aorta to the trunk and lower extremities.

The blood from the head and neck is returned to the right auricle by the superior vena cava. The blood from this vein passes through the auricle to the right ventricle, which sends it through the pulmonary artery towards the lungs.

The pulmonary artery, in the embryo, has one very large branch, called the ductus arteriosus, which joins the aorta at a point just below the origin of the vessels of the head and neck; hence the main part of the blood passing from the right ventricle reaches the aorta by the ductus arteriosus, and only a very small part goes to the lungs, to be returned from them by the pulmonary veins to the left auricle.

The blood from the ductus arteriosus blends, therefore, with that in the aorta which is passing to the viscera and lower extremities. The main part of this blood travels by two large branches of the aorta (the hypogastric arteries) to the placenta, where it is aerated and purified, &c.

It is evident if the placenta is the great renovating organ of the blood of the fœtus, that the blood in the umbilical vein is the most arterial in the fœtal circulation. The blood in the ascending vena

cava and first part of the aorta is likewise fairly arterial, but the blood in the descending aorta is of a mixed character, as it contains blood which has nourished the head and neck, besides that which has come from the placenta by the inferior vena cava through the right auricle, foramen ovale, left auricle, and left ventricle.

As the fœtal lungs are not called into play until after birth, but little blood passes to them in the fœtus; this state of things is however completely altered at birth, when the lungs of the child expand, the pulmonary arteries increase in size, and the ductus arteriosus dwindles in a corresponding degree.

The liver, which in the fœtus is of relatively greater size than in the adult, receives much blood coming from the placenta to the heart, and is thought to contribute to it several essential constituents.

The head and brain, which are largely developed in the fœtus, receive well aerated blood; namely, the placental blood which has passed through the liver, and, in the inferior vena cava, is mixed with blood coming from the lower limbs. The rest of the fœtus receives blood that is less well aerated, as it is mixed with that which is returned from the head and neck to the right side of the heart, and which is sent through the ductus arteriosus to join the general blood current in the aorta going to the viscera and lower extremities.

Development of the Eye.

The optic vesicles arise from the anterior cerebral vesicle at a very early period, and their cavities are continuous with that of the fore-brain. With the development of the rudimentary cerebral hemispheres the optic vesicles become displaced downwards, and their cavities open into the junction of the cavities of the cerebral hemispheres, and that of the thalamencephalon, which becomes the third ventricle. Later, the optic vesicles open directly into the third ventricle, and finally are displaced backwards, and come into connection with the mid-brain.

The optic vesicles are at first hollow prolongations, which consist of an anterior dilated portion, forming the primary optic vesicle, and a posterior tubular portion or stalk joining the vesicle to the fore-brain. This stalk forms the optic nerve.

As each vesicle grows forward towards the epiblast covering the head of the embryo, the epiblastic cells at the spot overlying the vesicle become thickened, an involution of the epiblast takes place

towards the optic vesicle, and indents the latter, approximating its anterior to its posterior wall.

By this means the anterior and posterior walls of the primary optic vesicle come into close contact, and the cavity of the vesicle is obliterated. The two layers of the vesicle are now cup-shaped, and receive the name of the secondary optic vesicle or the *optic cup.* This ultimately becomes the retina, and the optic stalk losing its cavity, is transformed into the optic nerve.

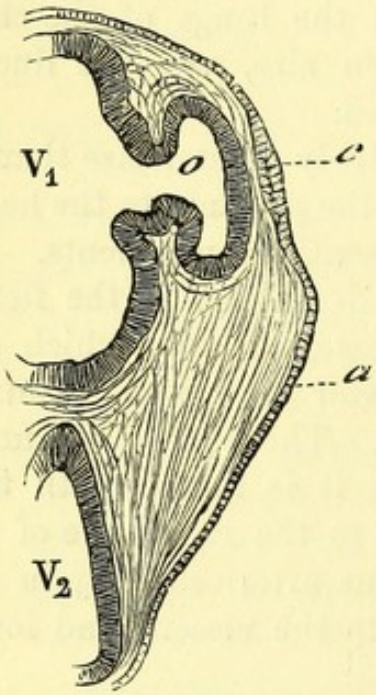


Fig. 309.—Section through the head of a chick at the third day, showing the origin of the lens.

a. Epiblast thickened at *c*, which is the point of origin of the lens.

o. Optic vesicle.

V 1. Anterior cerebral vesicle.

V 2. Posterior cerebral vesicle.

Meanwhile, the local involution of the epiblast over the optic cup, which is the rudiment of the crystalline lens, becomes gradually separated from the general epiblast, and is finally detached from its point of origin. It now lies as a somewhat spherical body in the cavity of the optic cup within the superficial mesoblast, which has closed over it.

The secondary optic vesicle grows (except at its lower part, just at the junction of the optic stalk), so as to deepen the optic cup, which contains the rudimentary lens. At the lower part an interval is left, which receives the name of the *choroidal fissure.* Through this gap in the secondary optic vesicle the mesoblast enters and separates the lens from the optic cup, forming the vitreous humour.

The mesoblast surrounding the optic cup develops two coverings of the eye, an outer fibrous capsule called the sclerotic coat, and a vascular coat, the choroid.

In front of the lens, beneath the epiblast, the mesoblast forms the corneal tissue proper. The epiblast forms the epithelial or conjunctival covering of the eyeball.

The involution of mesoblast through the choroidal fissure, which forms the vitreous humour, indents the optic stalk, and forms the central artery of the retina. The choroidal fissure is gradually obliterated, and its position may sometimes be marked by a permanent fissure in the iris (*coloboma iridis*). The rudimentary lens is a spherical body, hollow in the centre, made up of an anterior and

posterior wall, each of which is formed of columnar cells. The posterior wall of the lens increases greatly in thickness, and approaching the anterior obliterates the original cavity of the lens.

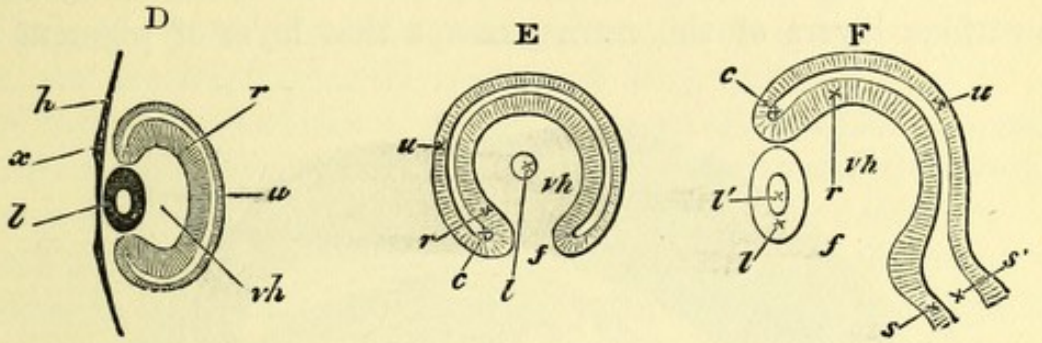


Fig. 310.—Diagrammatic sections of the primitive eye, showing the choroidal fissure. (Foster and Balfour.)

D. Horizontal section.
E. Vertical transverse section just striking the posterior part of the lens.
F. Vertical longitudinal section through the optic stalk, and the fissure through which the mesoblast passes to form the vitreous humour.

h. Superficial epiblast.
x. Point of origin of the lens.
v.h. Vitreous humour.
r. Anterior layer of the optic vesicle.
u. Posterior layer of the optic vesicle.
c. Cavity of the optic vesicle.
f. Choroidal fissure.
s. Optic stalk.
s'. Cavity of the optic stalk.
l. Lens. *l'*. Cavity of the lens.

The cells forming this wall become very much elongated, and develop into long fibre-like columnar cells. Those of the anterior

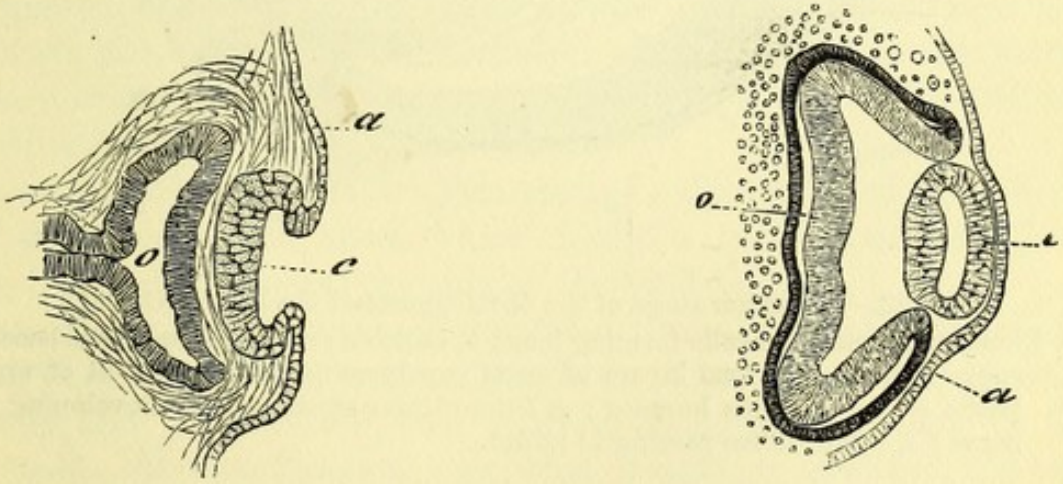


Fig. 311.—Later stages in the development of the lens. (Cadiat.)

a. Epiblast. *c*. Rudimentary lens. *o*. Optic vesicle.

wall from being a columnar, are modified to a flattened epithelium, and finally become the layer lining the anterior surface of the capsule, of the lens. The capsule of the lens has been variously considered as arising from the cells of the lens substance, or as originating from

a thin layer of mesoblast, which forms not only the lens capsule, but also the hyaloid membrane, which is continuous with it.

The optic cup gives origin to the retina. The inner or anterior layer of the cup becomes thickened, and from it are differentiated the various layers of the retina, except that layer of pigment cells

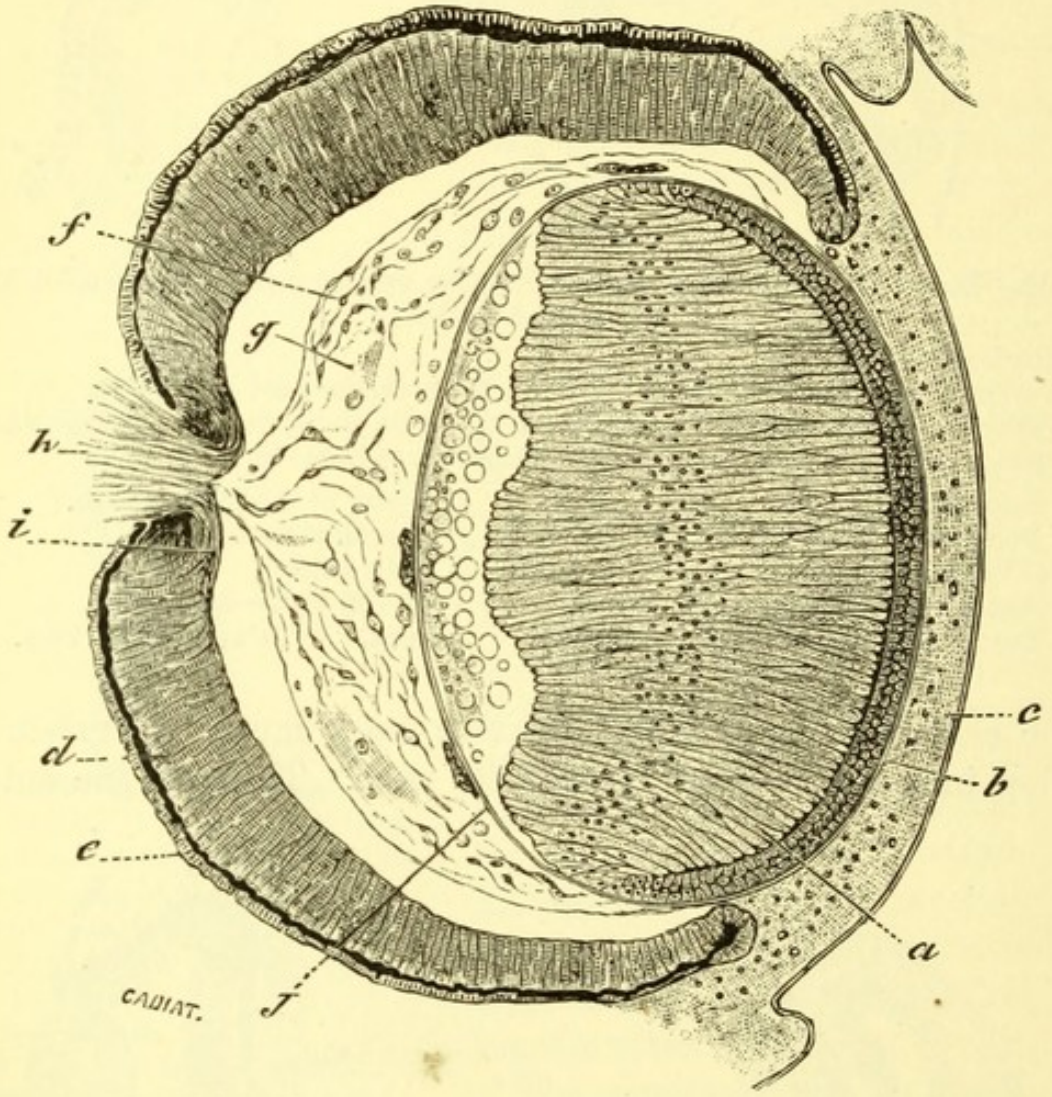


Fig. 312.—A further stage of the development of the lens. (Cadiat.)
a. Elongating epithelial cells forming lens; *b*, Capsule; *c*, Cutaneous tissue becoming conjunctiva; *d*, *e*, Two layers of optic cup forming retina; *f*, Cell of mucous tissue of the vitreous humour; *g*, Intercellular substance; *h*, Developing optic nerve; *i*, Nerve fibres passing to retina.

which lies next to the choroid. The posterior layer develops this layer of pigment cells, which, from their intimate connection to the choroid, were formerly considered as part of that membrane.

The thickening of the inner or anterior layer of the optic cup ceases at the ora serrata. The outer layer with its contiguous choroid is thrown into a number of folds—the ciliary processes—and passing in front of the lens, helps to form the iris.

In front of the ora serrata the anterior layer of the cup is no longer differentiated into the special retinal elements, but joins with the posterior to form a layer of columnar cells,—the *pars ciliaris retinæ*. In front of this the anterior rim of the optic cup passes forwards and lines the posterior surface of the iris, forming the uvea of that organ, and terminating at the margin of the pupil.

The rest of the substance of the iris is developed from the mesoblast, from which also arise the choroid, the cornea and the sclerotic.

The development of the eye may be thus briefly described. An offshoot of nervous matter from the fore-brain, forms the retina and the uvea, and its stalk, or connection with the brain, develops into the optic nerve.

An involution of epiblast which grows into the nervous cup forms the lens, whilst from the adjacent mesoblast arise the surrounding parts of the eye. The vitreous is produced by the mesoblast growing through a fissure in the lower part of the optic cup to fill its cavity.

Development of the Ear.

The ear is developed chiefly from the epiblast, a special and independent involution of which forms both its essential nervous structures, and the general epithelium lining the membranous labyrinth. The mesoblast supplies the surrounding firmer structures, such as the fibrous substance of the inner ear, and the bony parts in which the organ lies. The auditory nerve grows as a bud from the neural tissue forming the hind-brain, and connects it with the delicate specialised auditory cells.

The process begins by the appearance of a depression of the general epiblast covering the head, which forms a tubular diverticulum, lying in the mesoblast at the side of the hind-brain.

This diverticulum becomes separated from the epiblast by the obliteration of its outer extremity, which united it to the superficial epiblast, and is converted into a cavity receiving the name of the *otic vesicle*. It soon becomes somewhat triangular in shape, the base of the triangle lying upwards.

From the lower angle arises a projection, which is the rudimentary canal of the cochlea. The angle lying next to the neural epiblast similarly gives off a tubular process, which forms the recessus vestibuli.

Elevations in the primitive vesicle indicate the origin of the semicircular canals, which become tubular, opening at their ends into the

general cavity of the vesicle. The two superior canals are the first to appear, the horizontal rising somewhat later.

The part of the otic vesicle in connection with the canal of the cochlea becomes separated from the latter by a narrow constriction which forms the canalis reuniens, the part of the vesicle beyond this developing into the saccule.

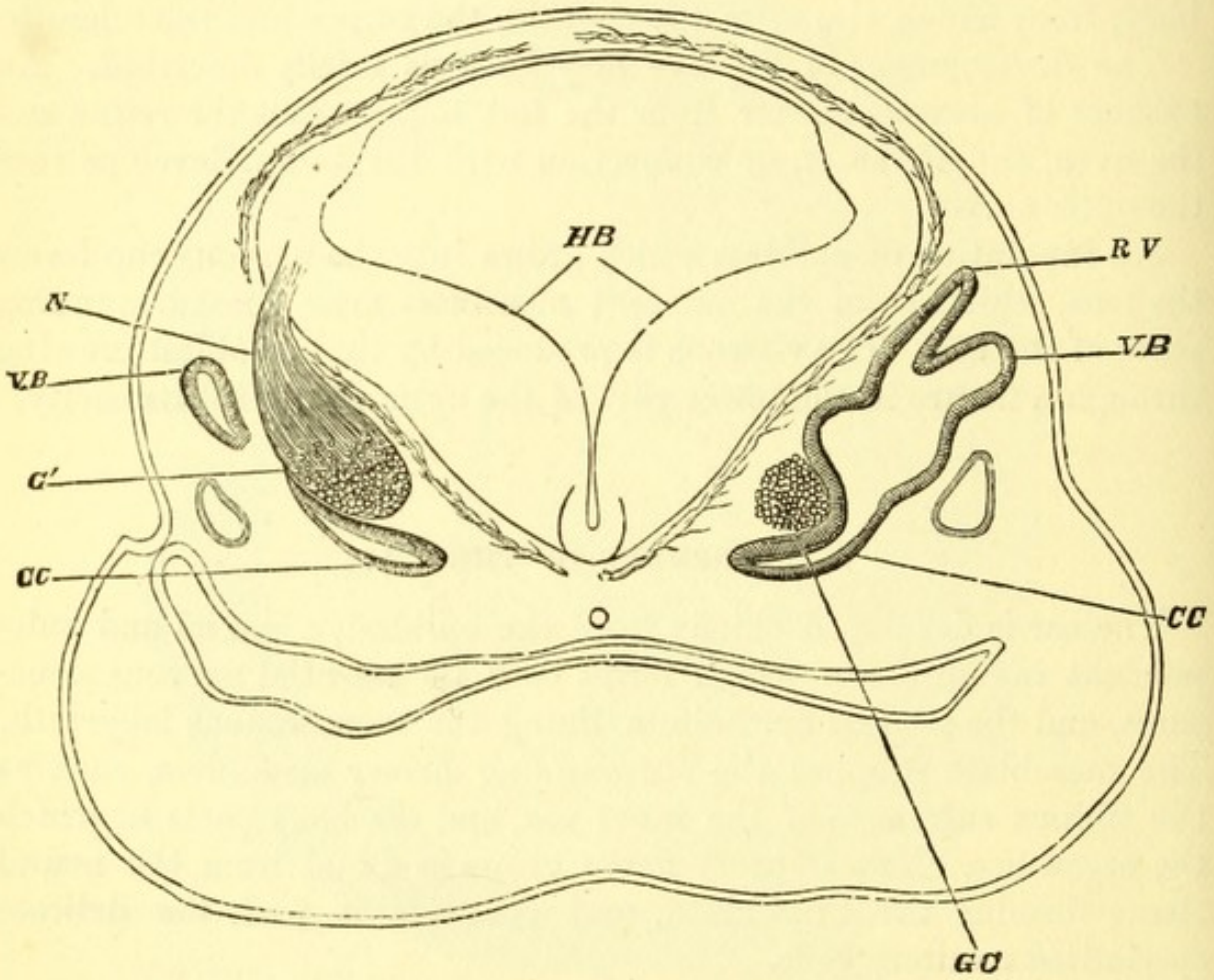


Fig. 313.—Transverse section through the head of a fœtal sheep in the region of the hind-brain. (Boettcher.)

H. B. Hind-brain.
CC. Canal of the cochlea.
RV. Recessus vestibuli.
VB. Vertical semi-circular canal.
G.C. Auditory ganglion.
G'. Auditory nerve.
N. Connection of auditory nerve to the hind-brain.

The utricle arises from that part of the vesicle which is in connection with the semi-circular canals. It is at first in direct connection with the saccule, but after a time it only communicates by means of a narrow canal with a similar one from the saccule; these two canals are connected with a third, which lies in the aqueductus vestibuli.

The canal of the cochlea is at first a straight tube, but as it develops it becomes coiled upon itself.

The walls of the primitive otic vesicle, formed from the epiblast, become developed into the epithelium lining the internal ear. The mesoblast immediately surrounding the vesicle forms a supporting capsule of fibrous tissue, which completes the membranous parts of the internal ear.

Part of the mesoblast around the otic vesicle becomes liquefied,

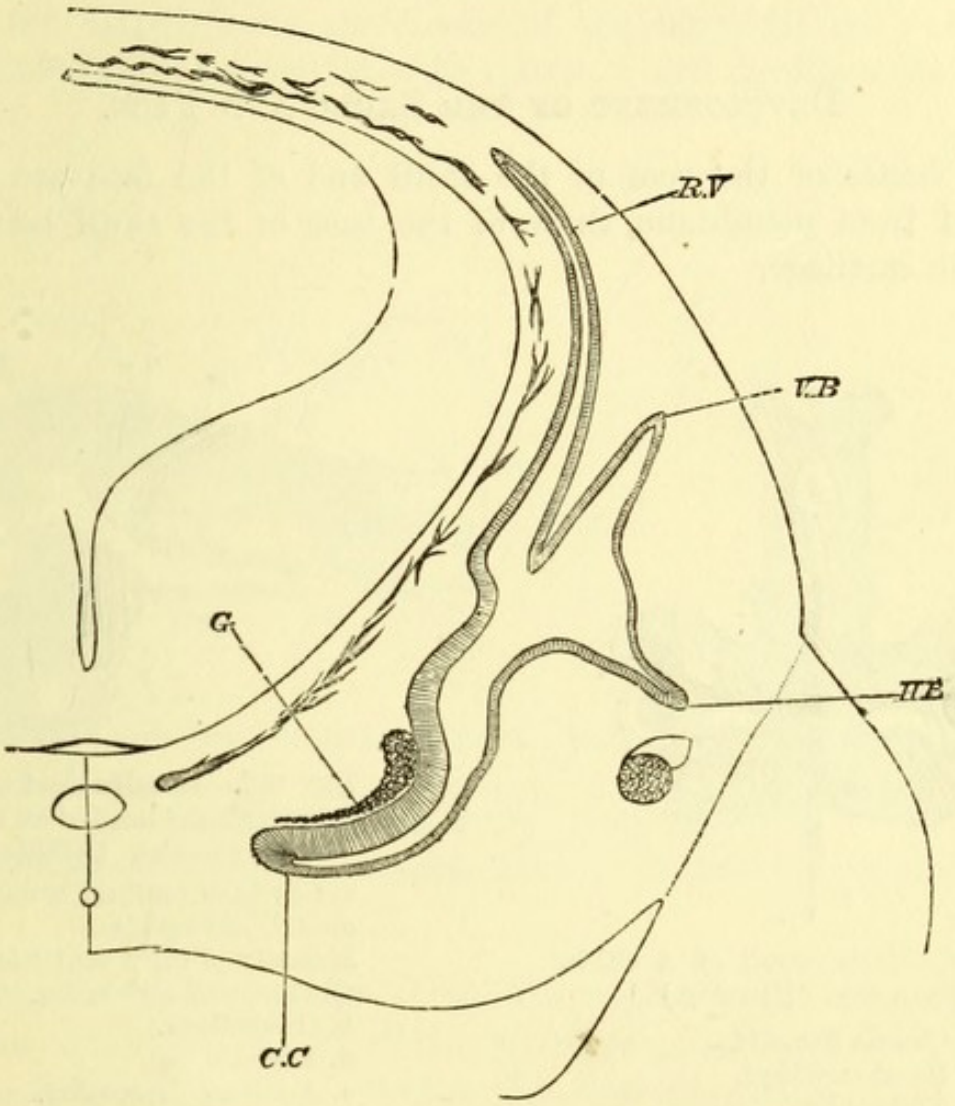


Fig. 314.—Section through the head of a fœtal sheep. (Boettcher.)

R.V. Recessus vestibuli.
V.B. Vertical semi-circular canal.
H.B. Horizontal semi-circular canal.
G. Auditory ganglion.
C.C. Canal of the cochlea.

and gives origin to the canals and spaces in which the membranous labyrinth lies, the neighbouring mesoblast is changed into cartilage which ossifies and forms the bony parts of the ear.

The auditory nerve is developed from the hind-brain, and grows through the mesoblast towards the otic vesicle. It is recognisable from its having some ganglion cells in its growing extremity from a very early period of its development.

The Eustachian tube and the tympanum are formed in connection with the inner part of the first visceral cleft, and the ossicles are developed from the corresponding visceral arch—*hyo-mandibular*.

The membrana tympani is formed at the surface of the embryo, the adjacent parts grow outwards and give rise to the external auditory meatus.

Development of the Skull and Face.

The bones of the roof of the skull and of the face are chiefly derived from membrane, those of the base of the skull being laid down in cartilage.

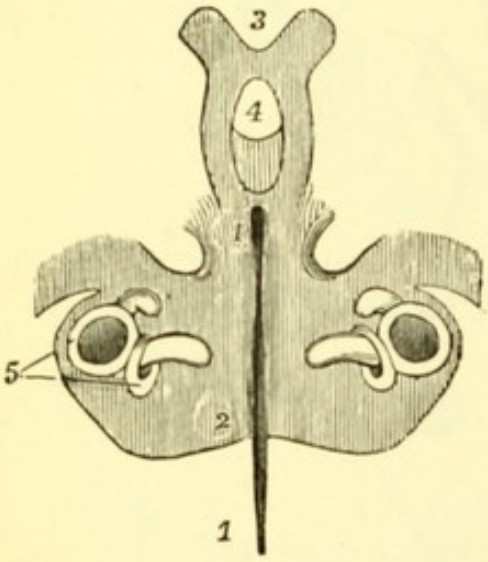


Fig. 315.—Basis cranii of a chick, sixth day. (Huxley.)

1. Chorda dorsalis.
2. Basal cartilage.
3. Trabeculæ.
4. Pituitary space.
5. Internal ear.

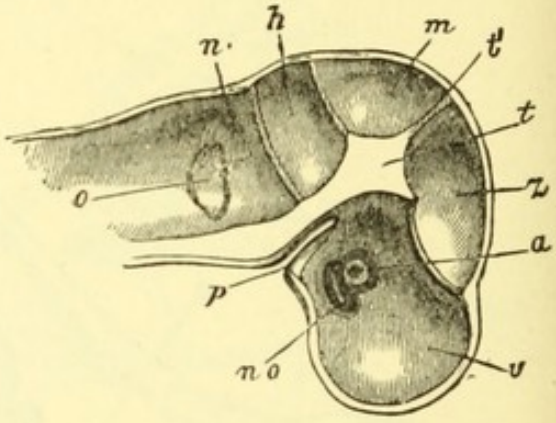


Fig 316.—Longitudinal section through the head of an embryo of four weeks. (Kölliker.)

v. Cavity of cerebral hemisphere.
a.no. Optic vesicle.
z. Cavity of third ventricle.
m. Cavity of mid-brain.
h. Cerebellum.
n. Medulla.
o. Auditory depression.
t. Basis cranii.
t'. Tentorium.
p. Pituitary body.

At the cephalic extremity of the notochord is a mass of uncleft mesoblast, called the investing mass, corresponding to that from which the vertebræ are developed.

From this arises two prolongations, which diverge and then unite again, leaving an interval; and the united portion becomes once more divided into two processes, the *trabeculæ cranii*.

The mesoblast behind the interval receives the name of the occipito-sphenoid portion; the interval is the rudiment of the sella tunica,

which is occupied by the pituitary body. The part of the mesoblast in front of this is called the spheno-ethmoidal portion.

From the occipito-sphenoidal portion are developed the basi-occipital and the posterior part of the sphenoid. At the sides of the medulla oblongata processes are sent up, which unite round it and form the foramen magnum. Laterally the mesoblast envelops the auditory vesicles and forms the side portions of the occipital bone.

In the cartilaginous antecedent of the temporal bone there are three centres of ossification—the *epiotic*, which develops the mastoid

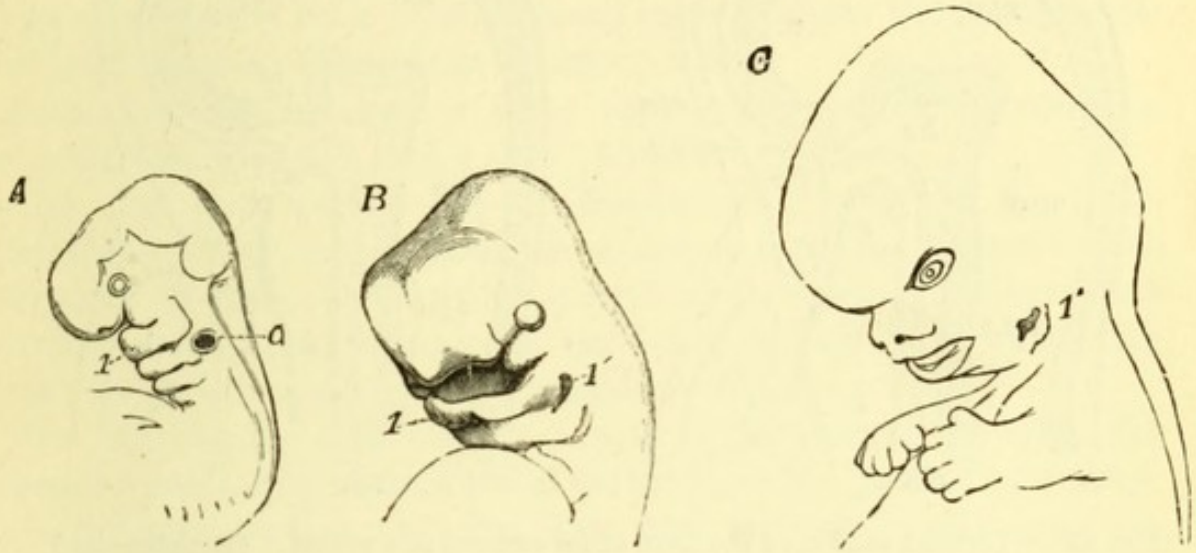


Fig. 317.—Different stages of the development of the head and face of a human embryo.

A. Embryo of four weeks. (Allen Thomson.) B. Embryo of six weeks. (Ecker.) C. Embryo of nine weeks. (Allen Thomson.)

a. Auditory vesicle. 1. Lower jaw. 1'. First pharyngeal cleft.

process; the *proötic*, which is in the region of the superior semi-circular canal; and the *opisthotic*, which is at the cochlea.

The spheno-ethmoidal portion develops the anterior part of the sphenoid together with the ethmoid bones and the cartilage of the septum of the nose, the first, arising from the back part, is developed from membrane. The trabeculæ are carried forwards, and bending down at the nasal depression form the lateral nasal cartilages and the anterior part of the septal cartilage.

The face is developed in connection with ridges known as the *visceral folds* or *arches*, between which are a number of clefts, the *visceral clefts*.

The eyes and the openings of the nose are in the face; whilst the ear arises at the side of the face, in connection with one of the visceral clefts.

The nasal depressions or pits appear in the wall of the head, covering the anterior part of the brain.

Just above the first visceral arch or fold is the depression which ultimately becomes the buccal cavity, and unites with the alimentary tract to form the mouth.

The first fold is called the mandibular; this gives off at either end

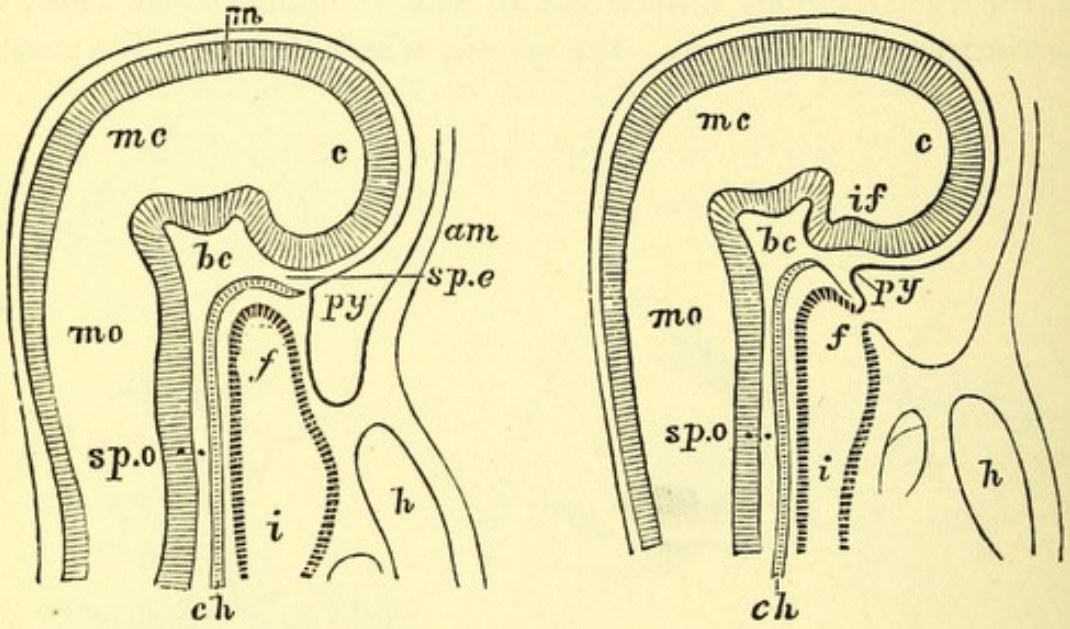


Fig. 318.—Vertical section of the head of an embryo of a rabbit. (Mihalkovics.)
In A. there is no connection between the buccal cavity and the foregut. In B. the connection is established.

m. Epiblast of neural canal.
h. Heart. *c*. Cavity of fore-brain.
mc. Cavity of mid-brain.
mo. Cavity of medulla.
sp.o. Spheno-occipital parts of the basis cranii.
sp.e. Spheno-ethmoidal part of the basis cranii.
bc. Part of basis cranii which receives the pituitary body.
am. Amnion.
py. Part of heart cavity going to form the pituitary body.
i.f. Fore-gut.
ch. Notochord.
if. Infundibulum.

a process which grows upwards and inwards, forming the rudiment of the superior maxillary bone and side of the face.

Between these is a median process, the fronto-nasal, which gives off, on the inner sides of the nasal grooves, projections which form the inner nasal processes; these unite with the superior maxillary processes to close in the nostril and form the lip.

The outer nasal process is a thickening on the outer side of the nasal depression, which running down towards the superior maxillary process, forms eventually the lachrymal duct.

The mandibular arch forms the lower jaw, and between this and the superior maxillary process the buccal cavity is developed chiefly

by the outgrowth of the surrounding tissue; the epiblast lining this becomes thinned away, and the subjacent mesoblast and hypoblast disappear; the buccal cavity is made continuous with that of the alimentary canal.

The cavities of the nasal depressions at first open freely into the buccal cavity by means of the nasal grooves; after a time processes arise from the superior maxillæ, and, growing inwards, finally meet one another in the middle line, to form a broad plate of tissue intervening between the nasal cavity above, and the buccal cavity below. This palate is first completed in front and then gradually closes towards the back of the buccal cavity, where the communication between the nose and the pharynx is left.

Imperfect development of these parts gives rise to the common congenital deformities, cleft-palate and hare-lip.

The first cleft is the *hyo-mandibular;* it forms the tympano-Eustachian cavity, which becomes separated from the surface by the closure of its outer end by the growth of the membrana tympani, the external auditory meatus and ear being formed by an outgrowth of the tissue surrounding the tympanic membrane.

The mandibular arch contains, close to its connection with the superior maxillary process, a rod of cartilage, called Meckel's cartilage. This becomes partly converted into the malleus, partly into the internal lateral ligaments of the temporo-maxillary articulation.

The second, or hyoid arch, gives origin to the incus, the stylo-hyoid process and ligament, and the lesser wings of the hyoid bone.

From the third arch arise the body and greater wings of the hyoid bone and the thyroid cartilage.

GLOSSARY.

Abscissa. The line forming the basis of measurement of graphic records, along which the time measurement is usually made.

Accommodation. Focussing the eye for different distances; it is effected by the lens becoming more convex for near objects, owing to the ciliary muscle drawing forward its choroidal attachment, and relaxing the suspensory ligament.

Acinous glands. Secreting organs composed of small saccules filled with glandular epithelium connected with the twigs of a branched duct.

Adenoid tissue. A delicate felt-work of reticular tissue containing lymph corpuscles (Lymphoid tissue).

Adequate stimulus. The particular form of stimulus which excites the nerve-endings of a special sense organ.

Afferent nerves. Those bearing impulses to the nervous centres from the periphery to excite reflex actions or stimulate the sensorium.

Agminate glands. A name applied to the lymph-follicles occurring in groups in the lower part of the small intestine.

Albumins. A term derived from the Latin for white of egg (*albumen*), denoting a group of complex chemical substances obtained from ova, blood-plasma, and many tissues of animals and plants.

Albuminoids. A class of nitrogenous substances allied to the albumins in composition, but differing from them in many important respects.

Allantois. A vascular out-growth from the embryo; in mammals it helps to form the placenta, and in the chick becomes the respiratory organ.

Alveoli. The term used to denote small cavities found in many parts, such as the air spaces of the lungs.

Amnion. The membranous sac which grows around the embryo and encloses the fœtus, &c., during its development.

Amœba. A unicellular organism consisting of a nucleated mass of protoplasm.

Amorphous. Without definite or regular form; the opposite of crystalline.

Ampulla. A dilatation on the semi-circular canals of the ear.

Amylolytic. Relating to the conversion of starch into dextrine and grape sugar.

Amylopsin. A ferment in the pancreatic juice, which converts starch into sugar.

Anabolic. An exciting influence exerted by nerves increasing the metabolism of tissues.

Analgesia. A condition of the nervous centres in which pain cannot be felt, but tactile and other sensations remain unimpaired.

Analysis. A separation into component parts; the splitting up of a chemical compound into its constituents.

Anastomoses. The direct union of blood-vessels without the intervention of a capillary network.

Anelectrotonus. An electric condition of a nerve, resulting from the passage of a current through a part of it ; it is confined to the region of the positive pole.

Anode. The positive pole or electrode—*i.e.*, the pole by which the electric current enters.

Apnœa. A state of cessation of the breathing movements from non-excitation of the respiratory nerve centre.

Area opaca. The outer zone of the part of the blastoderm from which the fœtal membranes are developed.

Area pellucida. The central spot of the part of the blastoderm from which the embryo chick is developed.

Arteriole. A small artery ; usually applied to those vessels the walls of which are largely composed of muscle tissue.

Arthroses. Movable joints having a synovial membrane.

Asphyxia. Literally, cessation of the pulse, such as occurs from interruption of respiration, now used as synonymous with suffocation.

Assimilation. The chemical combination of new material (nutriment) with living tissues. Power to assimilate forms the most characteristic property of living matter.

Astigmatism. Unevenness of the refracting surfaces of the eye ; when engaging the entire cornea it is called "regular," and affecting a local part, "irregular" astigmatism.

Atoms. The ultimate indivisible particles of matter.

Atrophy. A wasting from insufficient nutrition.

Automatic. Self-moving—*i.e.*, acting without extrinsic aid ; a term applied to the independent activity of certain tissues (such as the nerve centres), the exciting energies of which are not readily determined.

Axis cylinder. The essential conducting part of a nerve fibre, composed of fine strands of protoplasm.

Bacteria. A class of minute fungi occurring in decomposing animal or vegetable substances.

Bilirubin. The red colouring matter of the bile of man and carnivora.

Biliverdin. The greenish colouring matter of the bile of herbivorous animals.

Binocular. Pertaining to vision with two eyes. A combination of the effect of two retinal impressions by means of which the appearances of *distance* and *solidity* are arrived at.

Biology. The science of life, including morphology and physiology.

Blastoderm. The primitive cellular membrane formed by the segmentation of the ovum, in a part of which the embryo is developed.

Blood-pressure. The force exercised by the blood against the walls of the vessels. It is very great in the arteries, and therefore causes a constant stream through the capillaries to the veins.

Canaliculi. Minute channels connecting the small cell spaces or lacunæ of bone, and containing protoplasmic filaments uniting the neighbouring cells.

Carbohydrates. Compounds of carbon, hydrogen, and oxygen, in which the oxygen and hydrogen exist in the proportions requisite to form water.

Cardiograph. An instrument by means of which the heart's impulse is transmitted, through an air tube, from a tambour on the chest wall to another which makes a record on a moving surface by means of a lever.

Catelectrotonus. An electric state of nerve in the region where the current leaves the nerve, *i.e.*, near the negative pole.

Cathode. The negative pole or electrode—*i.e.*, the pole by which the electric current leaves.
Cellulose. The substance of which vegetable cell-walls are formed.
Centrifugal. Efferent.
Centripetal. Afferent.
Cerebral vesicles. Primitive swellings on the primary neural tube of the early embryo which develop into the brain.
Chemical elements. Substances which cannot be split up into components, and therefore are regarded as simple.
Chlorophyll. The green colouring matter of the cells of plants. It is supposed to be the agent which, under the influence of light, decomposes carbon dioxide and water to form the cellulose and starch of the plant.
Cholesterin. A substance occurring in the bile, white matter of the brain and spinal cord, and in small quantities in many other tissues. Chemically it is a monatomic alcohol.
Chorda dorsalis. The precursor of the vertebral column of the embryo.
Chorion. The outer layer of the membranes of the ovum, part of which becomes vascular, and helps to form the placenta.
Choroid. The vascular coat of the eye-ball.
Chromatic aberration. The alteration of white light into prismatic colours during its passage through an ordinary lens.
Chyle. The fluid absorbed from the small intestines by the lacteals.
Chyme. The fluid formed by gastric digestion.
Cilia. Minute vibratile processes which occur on the surface cells of the respiratory and many other epithelial membranes.
Circumvallate. Large papillæ situated at the back of the tongue. They are surrounded by a fossa in the walls of which lie taste buds.
Cloaca. The opening common to the genito-urinary organs into the primitive hind gut of the embryo. The cloaca persists in birds.
Colloid. That condition of quasi-dissolved matter in which it will not diffuse through a membrane such as parchment. The opposite of *crystalloid.*
Colostrum. The first milk secreted after delivery.
Co-ordination. The adjustment of separate actions for a definite result, as when the nerve-centres cause various distinct muscles to act together and produce complex movements.
Curara. A poison causing motor paralysis by impairing the function of the nerve terminals.
Cytod. A living protoplasmic unit which has no nucleus.

Decidua reflexa. The outgrowth of the uterine mucous membrane which surrounds the ovum.
Decidua serotina. That part of the modified mucous membrane of the uterus in which the fecundated ovum is lodged.
Decidua vera. The altered mucous membrane of the uterus, which lines that organ during gestation.
Deglutition. The act of swallowing.
Desquamation. The term used to denote the casting off of the outer layer of the skin.
Dialysis. The diffusion of soluble crystalloid substances through membranes such as parchment.
Diastole. The period of relaxation and rest of the heart's muscle.
Dicrotic. The double wave of the arterial pulse. The dicrotic wave is seen on the descending part of the pulse curve.

Dioptric media. Transparent bodies, such as those parts of the eye which so refract the light that images come to a focus on the retina.

Discus proligerus. Part of the granular layer of the Graafian follicle surrounding the ovum.

Distal. A term used to denote a part relatively far from the centre.

Ductus arteriosus. A short bond of union between the pulmonary artery and the aorta, which in the fœtus carries blood from the right side of the heart into the aorta.

Ductus venosus. A vessel which, in the fœtus, carries blood from the umbilical vein to the vena cava. After birth it becomes a fibrous cord.

Ductus vitello-intestinalis. The union between the yolk sac and the intestine of the embryo.

Dyspnœa. Difficulty of breathing; a condition in which inordinate respiratory movements are excited by an unusually venous state of the blood in the respiratory nerve centre.

Ectoderm. The outer layer of simple organisms.

Ectosarc. The outer layer or covering of certain unicellular organisms.

Electrodes. The terminals which are applied to a substance in order to complete the circuit in passing a current through it.

Electrotonus. A peculiar electric state of nerves resulting from the passage of a continuous current through them.

Embryo. The name given to the animal at the earliest period of its development.

Emmetropic. A term applied to the normal eye, in which parallel rays of light are brought to a focus at the retina without accommodation.

Emulsification. The suspension of very fine particles in a liquid unable to dissolve them.

Endoderm. The inner layer of simple organisms.

Endogenous reproduction. The formation of new cells or organisms within the body of the parent individual.

Endolymph. The liquid contained within the membranous labyrinth of the ear.

Endosarc. The inner layer of certain unicellular organisms.

Endosmosis. The diffusion of a fluid into a texture.

Endothelium. The single layer of thin cells lining the serous cavities, lymphatic and blood-vessels, and all spaces in the connective tissues (mesoblastic lining cells).

Epiblast. The uppermost of the three layers of the blastoderm, from which are developed the epidermis and the nerve-centres.

Epithelium. The non-vascular cellular tissue developed from the epi- and hypoblast of the blastoderm.

Eupnœa. A term used to denote the normal rhythm of respiratory movements in contradistinction to *dyspnœa* and *apnœa*.

Excito-motor. Impulses which, reflexly, call forth motion.

Excito-secretory. Impulses calling forth the activity of gland cells, commonly applied to afferent influences which act reflexly.

Fibrinogen. A form of globulin obtained from serous fluids, which, on being added to a liquid containing serum-globulin, gives rise to the formation of fibrin.

Fibrinoplastin. A term sometimes applied to paraglobulin or serum-globulin.

Filiform. A name given to a class of papillæ of the tongue, the points of which taper off to a thread.

Fœtus. The fully-formed embryo while in the uterus or egg.
Fovea centralis. The depression in the centre of the *macula lutea.*
Fungiform. A class of papillæ of the tongue shaped like a toadstool.

Galvanometer. An instrument for measuring the direction and strength of electric currents by means of the deflection of a magnetic needle.
Ganglion. A swelling. Chiefly used to denote swellings on nerves containing nerve corpuscles. Hence any group or mass of nerve cells.
Gastrula. A stage in the development of animals in which they consist of a small sac composed of two layers of cells.
Gemmation. Budding—a process of reproduction in which a bud forms on the parent organism, and finally separates as a distinct being.
Globulin. A form of albumin insoluble in pure water but soluble in weak solutions of common salt.
Glomerulus. A bundle of capillary loops which form part of the Malpighian body of the kidney.
Glycocholic acid. An acid existing in large quantities combined with soda in the bile of man.
Glycogen. Animal starch ; a substance belonging to the carbohydrates, which is made in the liver. It may be readily converted into grape sugar—from which fact it derives its name.
Gustatory. Pertaining to the sense of taste.

Hæmatin. A dark-red amorphous body containing iron ; obtained from the decomposition of the colouring matter of the blood (hæmoglobin).
Hæmatoin, or **Hæmatoporphyrin.** Iron-free hæmatin prepared with strong acetic acid.
Hæmatoidin. A substance found in old blood clots, as crystals, which cannot be artificially prepared.
Hæmin. Hydrochlorate of hæmatin ; easily obtained, as small dark crystals, by boiling blood to which some common salt and glacial acetic acid have been added.
Hæmochromogen. Unoxidised hæmatin, the first outcome of the decomposition of hæmoglobin.
Hæmoglobin. Reduced oxyhæmoglobin.
Holoblastic. The form of ova the entire yolk of which enters into the process of segmentation.
Homœothermic. Even temperatured—a term applied to those animals that keep up a regular temperature, independent of their surroundings—warm-blooded animals.
Hyaloid. Glass-like ; a name given to the delicate membrane enclosing the vitreous humour.
Hydrocarbons. Compounds of carbon and hydrogen. Fats, though containing oxygen in addition, have been called hydrocarbons.
Hypermetropia. The condition in which the focus of parallel rays of light lies beyond the retina ; also called *long sight.*
Hypertrophy. Increased growth from excessive nutrition.
Hypoblast. The undermost of the layers of the blastoderm, from which the pulmonary and alimentary tracts and their glands are formed.

Infusoria. A name given to a large class of simple organisms which are found in dirty water.
Inhibition. A checking or preventive action exercised by some nervous mechanisms over nerve corpuscles and other active tissues.

Inosit. A sugar peculiar to muscle.

Irradiation. The phenomenon that bright objects appear larger than they really are. It is due to the extension of the effect to those parts of the retina immediately adjacent to where the light rays impinge.

Karyokinesis. A series of changes occurring in the arrangement of the nuclear network prior to the division of the protoplasm of cells.

Katabolic. A lowering influence exerted by certain nerves, decreasing metabolism. Inhibitory action.

Keratine. The characteristic chemical constituent of the horny layer of the skin and epidermal appendages.

Kymograph. An instrument used for recording graphically the undulations of blood-pressure, measured directly from a blood-vessel by means of a manometer.

Lachrymal. Pertaining to the secretion of tears.

Lacunæ. Small spaces in the substance of bone tissue, occupied during life by the bone-cells. They appear black in sections of dry bone owing to their containing air, which replaces the shrivelled cells.

Latency, or Latent period. The time that elapses between the moment of stimulation and the response given by an active tissue.

Leucin. This is a common product of the decomposition of proteids. It is formed in the later stages of pancreatic digestion.

Leucocytes. A term applied to the white blood-corpuscles and lymph cells.

Lumen. The open space seen on section of a tube, vessel or glandular saccule; the cavity surrounded by the gland-cells, in which the secretion collects.

Luscitas. Fixation of the eye-ball in the outer canthus owing to the unopposed action of the external rectus muscle.

Lymph. The liquid collected by the absorbent vessels from the tissues; the return flow of the irrigation stream escaping from the blood-vessels to nourish the tissues.

Macula Lutea. That part of the retina near the axis of the eyeball, in which vision is most acute.

Manometer. An instrument for measuring pressure; made of a U-shaped tube containing liquid, commonly mercury.

Medullary sheath. A soft clear sheath around the axis cylinder of medullated nerves, which, owing to its refracting power, gives them a white appearance.

Menstruation. The monthly change in the mucous membrane of the uterus, which accompanies the discharge of the ovum.

Meroblastic. The form of ova in which the yolk does not undergo complete segmentation, as that of birds.

Mesencephalon. Those parts of the brain developed from the middle cerebral vesicle, viz., crura cerebri and corpora quadrigemina.

Mesoblast. The middle of the three layers of the blastoderm from which the connective tissues and vascular apparatus of the embryo are formed.

Metabolism. The intimate chemical changes occurring in the various organs and tissues upon which their nutrition and functions depend.

Metanephros. The hinder portion of the Wolffian body which develops into the kidney and ureter.

Metazoa. A term used to denote all those animals whose ova undergo division, in contradistinction to Protozoa.

Methæmoglobin. A compound formed by oxyhæmoglobin combining more firmly with additional oxygen.
Micrococcus. An extremely minute fungus of a round shape. Micrococci occur in many solutions of decomposing organic matter.
Micturition. The act of voiding urine.
Molecules. The smallest physical particles of matter that can exist in a separate state. They are probably always constituted of two or more atoms.
Morphology. The science which treats of the forms and structure of living beings.
Morula. The stage of development of the ovum after segmentation in which all the young cells are alike, before the blastoderm is formed.
Mucin. The characteristic constituent of mucus.
Mullerian duct. An embryonic structure from which are formed the genital passages in the female, viz., Fallopian tube, uterus, and vagina.
Mydriasis. A dilated state of the pupil.
Myograph. An instrument for graphically recording muscle contraction.
Myopia. The condition in which the focus of parallel rays of light falls short of the retina : *short sight.*
Myosin. The substance formed by the coagulation of muscle plasma. It is one of the globulins.

Natural nerve currents. The electrical currents passing through an exposed muscle or nerve while in a state of rest.
Neuroglia. The reticular connective tissue which binds together the elements of the nerve-centres.
Non-polarizable electrodes. Electric terminals specially constructed so as not to set up secondary currents on application to moist living tissues.
Notochord. The primitive vertebral axis of the embryo.
Nucleolus. A small spot observable in some nuclei.
Nucleus. A central part of a cell differentiated from the main protoplasm, commonly round, but sometimes elongated as in muscle.

Odontoblasts. Living cells lining the pulp-cavity of the interior of a tooth, and presiding over the growth and nutrition of the dentine.
Olfactory. Pertaining to the sense of smell.
Omphalo-mesenteric. The vessels connecting the embryonic circulation with the yolk sac, which are early obliterated in the mammalian fœtus.
Ophthalmoscope. An instrument consisting of a small mirror by which the interior of the eye can be illuminated so that the fundus may be viewed.
Optic cup. The involuted optic vesicle which is developed into the retina, &c.
Osteoblast. The active cells in forming bone.
Osteoliths. Calcareous particles lying in the endolymph.
Oxyhæmoglobin. The colouring matter of the blood-corpuscles.

Paraglobulin. One of the more abundant albumins of the blood — *serum globulin.*
Paramæcium. A unicellular organism composed of a soft mass of protoplasm enclosed in a firmer case, and covered with motile cilia.
Parapeptone. A body produced in gastric digestion during the formation of peptone.
Pepsin. A ferment existing in the gastric juice which converts proteids into peptones.

Peptone. A form of albumin which is produced during the digestion of proteids; it is very soluble, and diffuses readily through a membrane.

Perilymph. The liquid surrounding the membranous labyrinth of the ear.

Peristalsis. The mode of contraction of the muscular walls of certain tubes, as the œsophagus and intestine, the effect of which is to cause a progressive constriction, and so force the contents of the tube onwards.

Phakoscope. An instrument for estimating the changes in the shape of the lens during accommodation by doubling the reflected images with a prism.

Placenta. The intra-uterine organ by means of which the fœtal blood is brought into close relationship to that of the mother, so as to gain nutriment and oxygen, and get rid of effete matters.

Plasma. A term meaning anything formed or moulded; used in physiology to indicate chemically complex kinds of matter which subserve to the formation of the living tissues.

Poikilothermic. Varying in temperature. A term applied to those animals whose temperature varies with that of the surrounding medium—"cold-blooded animals."

Presbyopia. A loss of power of accommodation for near vision, which accompanies old age.

Prosencephalon. That part of the developing anterior cerebral vesicle from which are formed the olfactory and optic lobes, the hemispheres, and corpora striata and optic thalami.

Protista. A large group of organisms which remain in the primitive state of a single cell during their lifetime.

Protococcus. A unicellular vegetable organism, the protoplasm of which contains chlorophyll.

Protoplasm. The substance which gives rise to the primitive vital phenomena, seen in unicellular organisms, and which is the chief agent in executing the functions of all the active tissues.

Protovertebræ. The primitive segments of the mesoblast in the site of the future vertebral column.

Protozoa. That division of the protista which has been assigned to the animal kingdom.

Proximal. A term used to denote a part relatively nearer to the centre.

Pseudopodia. Projections thrown out by moving protoplasm, by means of which cells, such as amœbæ, move.

Ptosis. Drooping of the eye-lid accompanying paralysis of the third nerve.

Ptyalin. The ferment of the saliva. In a weak alkaline solution it converts starch into dextrine and sugar.

Reflex action. The activity caused by a ganglion cell reflecting an afferent impulse along an efferent nerve to the neighbourhood of original stimulation.

Reflexion. The return of rays of light from a surface.

Refraction. The bending which rays of light undergo when passing obliquely from one medium to another of different density.

Reticulum. A network; a term applied to the interlacement of fibres, seen in reticulated connective tissue, &c.

Rheoscopic frog. An arrangement by which the change in the electric current of one muscle of a frog is made to act as a stimulus to the nerve of another.

Saponification. The formation of soap; the decomposition of oils or fats by means of alkalies into salts of the fatty acid and glycerine.

Sarcolactic acid. The principal acid in dead muscle. It has a dextro-rotatory power on polarized light, which ordinary lactic acid does not possess.

Sarcolemma. The delicate sheath surrounding the fibres of skeletal muscles.

Sclerotic. The fibrous coat of the eye-ball.

Sensorium. That part of the nerve centres supposed to receive sensory impressions.

Somatopleure. The subdivision of the mesoblast which, with the attached epiblast, forms the body-walls of the embryo.

Specific gravity. The relation of the weight of a given volume of any substance to the weight of an equal volume of distilled water at 4° C.

Spherical aberration. An indistinctness of the image caused by the difference in refraction at the centre and margin of a lens giving rise to different focal lengths.

Sphygmograph. An instrument for obtaining a graphic representation of the pulse-wave by means of a lever applied to the radial artery at the wrist.

Splanchnopleure. The subdivision of the mesoblast which, with the attached hypoblast forms the chief visceral cavities of the embryo.

Sporadic ganglia. Swellings occurring in the course of the peripheral nerves caused by a group of nerve corpuscles.

Steapsin. A ferment existing in the pancreatic juice which causes or aids the saponification of the fats.

Sudoriferous glands. The small tubular glands of the skin which secrete perspiration.

Summation. The fusion of several single contractions of muscle to form a tetanic contraction; the accumulation of stimuli.

Sutures. Unions formed by the direct apposition of bones without intervening cartilage. They do not permit of motion.

Sympathetic nerve. The ganglionic nervous cord on either side of the vertebral column. It transmits most of the vaso-motor impulses coming from the cerebro-spinal centres.

Symphysis. A form of joint without synovial membrane in which the bones are fixed together by fibro-cartilage.

Synthesis. The artificial construction of a chemical compound from simpler materials.

Systole. The period of contraction of the heart's muscle.

Taurocholic acid. An acid existing in combination with soda in the bile.

Tetanus. In physiology is used to denote the prolonged contraction of the skeletal muscles which follows rapidly repeated stimulations or nervous impulse.

Thalamencephalon. That part of the anterior cerebral vesicle which is left after the differentiation of the optic thalami, cerebral hemispheres, &c.

Thrombosis. The occlusion of a vessel by a local coagulation of the blood.

Trabeculæ. Supporting bars of tissue passing through some organs, such as those proceeding from the capsule to the interior of the spleen or lymphatic glands.

Trophic. Relating to nutrition.

Trypsin. A ferment in the pancreatic juice which in alkaline solutions converts proteids into peptones.

Tyrosin. A substance formed together with leucin during pancreatic digestion; it is also produced by putrefaction of proteids.

Urachus. The bond of union which at an early period connects the urinary bladder with the allantois in the embryo; it is subsequently obliterated in the fœtus.

Vacuoles. Small cavities occurring in cells. They are supposed to have important functions in the unicellular organisms.

Vagus. The part of the eighth pair of nerves distributed to the viscera of the throat, thorax, and abdomen; the great regulating nerve of the vegetative functions.

Vaso-constrictor. Those impulses which excite contraction of the vascular muscles.

Vaso-dilator. Those impulses which inhibit the action of the vascular muscles.

Vaso-motor. Those nervous mechanisms controlling the movements of the blood-vessels.

Villus. A hair-like process. A term applied to the small projections characteristic of the small intestine. They contain blood-vessels and lacteals, and are important in absorption.

Vitellus. The yolk of the ovum, which in mammals divides completely to form the embryo. In birds only a part divides, and the rest serves to nourish the chick.

Vorticella. Bell animalcule, a bell-shaped unicellular organism with a rudimentary, ciliated mouth cavity and rapidly contractile stalk.

Wolffian body. An embryonic structure, the forerunner of certain parts of the genito-urinary apparatus.

Zymogen. A peculiar substance supposed to give rise to the pancreatic ferments.

INDEX.

Abdominal respiration, 276
Abductor nerve of the eye, 449
Abnormal constituents in the urine, 343
Absorbents of stomach, 112
Absorption, 149
— intestinal, 157
— interstitial, 151
— mechanism of, 161
Accommodation, 490
Acid albumin, 40
Acinous glands, 95
Active tissues, 17
Adipose diarrhœa, 164
Afferent nerve, 21, 426
Agminate glands, 161
Air passages of lung, 271
Albumin, acid, 40
— alkali, 41
— coagulated, 41
— conversion into peptone, 117
— egg, 39
— in the urine, 343
— serum, 39
— syntonin, 40
— tests for, 39
Albuminates, 40
Albuminoids, composition of, 42
Albuminous bodies, 38
— as food, 65, 67
Albumins, classification of, 39
— chemical composition of, 38
— characteristics of, 42
Alcoholic fermentation, 48, 59
Alimentary canal, 77
— development of, 608
Alkali albumin, 41
Allantoin, 46
Allantois, 590
Alveoli, 283
Amnion, 586
Amœba, 14
— change in form, 53
— effect of stimulation, 53
— life of, 60
— locomotion of, 53
— pseudopodia of, 53
Amœboid movement of white blood corpuscles, 182
Amount of blood in the body, 172
Amphioxus, blood of, 184
Ampullæ of semicircular canals, 525
Amylopsin, 128
Analgesia, 540
Anelectrotonus, 434
Animal heat, 363
— production of, 366
Anode, 431
Anterior roots of spinal cord, 533
Anus, 77
Apnœa, 289
Aortic arches, 627
— valves, 215
Area opaca, 584
— pellucida, 584
Arterial blood, 296
— pulse, the, 254
— system, development of, 626
— tone, 263
Arteries, small, 234
— walls of, 233
Arterioles, 235
Arthrosis, 408
Arytenoid cartilage, 416
Asphyxia, 303
Assimilation, 6

Astigmatism, 494
Atmospheric air, 293
Atoms, 5
Auditory nerve, stimulation of, 527
— terminals of, 524
Auerbach's plexus, 92
Augmentation, 443
Auricles, of the heart, 211
Automatic centres in spinal cord, 549
Automatism, 443, 549
Axis cylinder, 21, 425

Bacterium, 57, 58
Basilar membrane, 525
Battery, Daniell's, 429
Bell animalcule, 63
Bertin, columns of, 330
Bile, 129
— acids and pigments in the urine, 344
— cholesterine contained in, 137
— composition of, 135
— ducts, 134
— functions of the, 140
— method of obtaining, 135
— pigments, Gmelin's test for, 136
— salts, Pettenkofer's test for, 44, 137
— secretion of, 138
Biliary fistula, 135
Bilirubin, 137
Biliverdin, 137
Binocular vision, 514
Bladder, evacuation of the, 349
— nervous mechanism of, 547
— passage of the urine to the, 348
— structure of the, 349
Blastoderm, 12, 16, 582, 584
Blind spot, 504
Blood, action of re-agents on, 186
— amount of, 173
— arterial, 296
— buffy coat of clot, 200
— carbon dioxide in the, 198
— changes during respiration, 296
— changes in the, 186
— changes in the spleen, 312
— chemistry of the colouring matter, 190
Blood, chemistry of the stroma, 195
— circulation of the, 209
— circulation in frog's web, 262
— circumstances influencing coagulation, 201
— clot, 200
— coagulation of the, 199
— coagulation within the vessels, 203
— colourless corpuscles, 181
— colourless corpuscles, origin of, 183
— composition of, 172
— constitution of the, 171
— corpuscles, 174, 180
— corpuscles, increase in number of white, 181
— corpuscles, number of, 180
— corpuscles, separation from plasma, 175
— crenated red corpuscles, 186
— current, velocity of the, 259
— defibrinated, 200
— density of the, 186
— development of red discs, 196
— enumeration of blood-corpuscles, 188
— fibrin formation in, 205
— fibrin of, 175, 178, 200
— fibrinoplastin of, 178
— fibrin in, of, 179
— gases in the, 197, 299
— hæmatin of, 194
— hæmatoidin of, 195
— hæmin of, 195
— hæmochromogen of, 194
— lakey, 187
— methæmoglobin of, 194
— of amphioxus, 184
— of cold-blooded animals, 205
— origin of colourless corpuscles of, 183
— oxygen in the, 199
— oxyhæmoglobin of, 190
— -plasma, coagulation of, 176
— -plasma, chemical composition of, 176
— preparation of oxyhæmoglobin, 191
— red corpuscles of, alteration in shape, 186
— red corpuscles, 184

Blood, red corpuscles forming rouleaux, 186
— red corpuscles of, relative size in different animals, 185
— red corpuscles, shape in different animals, 185
— -serum, composition of, 179
— specific gravity of the, 172
— spectra of, 298
— spectra of hæmoglobin, 193
— stroma of the, 187
— thrombosis, 204
— venous, 296
Blood-pressure, 240
— influence of respiration on, 249
— in the pulmonary circulation, 254
— in the capillaries, 253
— in the veins, 253
— measurement by Fick's spring manometer, 250
— measurement by mercurial manometer, 244
— record of, 247
— tracing of, 243, 251
— relative height of, 247
— respiratory wave of, 249
— variations of, 248
Blood-vessels, 233
— clotting of blood in the, 205
— action of depression nerve on, 265
— nervous control of the, 267
— relative capacity of, 237
— vaso-motor centres of, 264
— vaso-motor nerves of, 263
Bone, 30
— composition of, 30
— growth of, 32
Brain, development of, 559, 605
— effect of stimulation of, 569
— fibres and cells in the, 567
— functions of the, 571
— recovery after injury of, 572
— result of removal of parts of, 570
— structure of, 558
— ventricles of, 552, 565
— volition, 549
Breaking shock, 431
Bronchial tubes, 272
Brownian movement, 52
Brunner's glands, 142
Butter as food, 72

Calabar bean, 492
Calculi, urinary, 344
Camera obscura, 484
Canaliculi of bone, 30
Capillaries, 235
— lymphatic, 156
Carbohydrates, 47
— as food, 65, 67
Carbon, 6
Carbon dioxide in the blood, 198
Carbonates in the tissues, 50
Carbonic acid, 294
Carbonic acid gas CO_2 in the tissues, 50
Cardiac centre, 557
— cycle, 218
— impulse, 221
— movements, 220
— nerve mechanism, 228
Cardiograph, 222
Cartilage, 29
Casein, 41, 323
Catelectrotonus, 434
Cathode, 431
Cell-contents, 9, 11
Cell-sap, 9
Cell-wall, 8, 10
Cells, animal, 8
— budding of, 55
— development of, 55
— differentiated, 13
— division of, 55
— fat-, 11
— ganglion-, 22, 447
— germination of, 55
— goblet-, 158
— history of, 8
— indifferent, 12
— liver, 9
— of mucous tissue, 27
— nerve, 22, 447
— nucleus and nucleolus of, 9
— pigment, 12
— reproduction of, 55, 57
— varieties of, 12
— vegetable, 8
Cellular theory, 8
Cellulose, 59
Centrifugal nerves, 424
Centripetal nerves, 424
Cereals as food, 74

Cerebellum, 562
Cerebral hemispheres, 568
— functions, localization of, 571
Cerebrospinal axis, 530
Cerebrum, 561
Chalaza, 582
Cheese as food, 72
Chemical stimulation of muscle, 385
— of nerve, 429
Chemistry of the body, 34
Chloride of sodium in the urine, 342
Chlorophyll, 59
Cholesterin, 45, 137
Cholin, 45
Chondrin, 43
Chorion, 591
Choroid, 478
Chromatic aberration, 493
Chyle, 152
— characters of, 165
— movement of, 170
— quantity of, 166
Cicatricula, 582
Ciliary ganglion, 453
— processes, 478
Ciliated epithelium, 19
Circulation of the blood, 208
— physical forces of the, 239
Circumvallate papillæ, 95, 474
Cleft palate, 641
Clot of blood, 176
Coagulation of the blood, 175, 199
Cochlea, 524
— canal of the, 525
— organ of Corti in, 525
Cold-blooded animals, 363
Colostrum, 323
Colourless blood-corpuscles, origin of, 183
Colourless corpuscles of blood, 181
Colour blindness, 511
— perceptions, 509
Columnar epithelium, 20
Common salt in the urine, 342
Composition of lymph, 166
— of the blood, 172
Connective tissue, 11
— tissues, classification of, 25
Constitution of the blood, 171
Constrictors of pharynx, 81
Continuous current, 386
Contractile tissues, 375
Convulsions, 303
Co-ordination, 442, 548
Cornea, 478
— nitrate of silver staining, 155
Corpora quadrigemina, 552
— striatum, 552, 565
Corpus collosum, 552
Corpuscles, blood, 174, 180
— enumeration of blood, 189
— lymph, 167
Corti, organ of, 525
Costal respiration, 276
Coughing, 292
Cranial nerves, 546
Cricoid cartilage, 416
Crusta petrosa, 78
Crying, 292
Crystallin, 40
Crystalline lens at different periods, 482
— fibres of, 484
Crystals of hæmoglobin, 191
Curara, 385
Cutaneous desquamation, 328
Cytode, 9

Daniell's battery, 429
Decidua reflexa, 592
— serotina, 592
— vera, 592
Defæcation, mechanism of, 90
Deglutition, 79
— nervous mechanism of, 84
Dentine, 78
Depressor nerve, 232
— action of, on blood-vessels, 265
Derived albumins, 40
Development, 595
— of alimentary canal, 608
— arterial system, 626
— blood vascular system, 619
— brain, 559, 605
— cells, 55
— ear, 635
— endothelium, 32
— eye, 482, 631
— genito-urinary apparatus, 612
— heart, 621
— kidneys, 616
— liver, 611

Development of lungs, 612
— nose and mouth, 640
— œsophagus, 612
— pancreas, 611
— red blood corpuscles, 196
— sexual organs, 618
— skull and face, 639
— spinal cord, 599
— spleen, 611
— venous system, 629
Dextrose, 47
Diaphragm, 278
Diastole of heart, 219
Diet tables, 361
Differentiated cells, 13
Digestion, alimentary tract, 77
— defœcation, 90
— deglutition, 79
— glands of stomach, 112
— mastication, 78
— mechanism of, 76
— movements of the intestines, 88
— small intestine, 142
— stomach, 85
Discus proligerus, 580
Division of egg cell, 56
Drum of ear, 520
Du Bois Reymond's induction coil, 386, 431 ; myograph, 392
Ductless glands, 306
Ductus arteriosus, 629
— venosus, 625
Ducts of Cuvier, 628
Duodenum, 77, 142
Dyspnœa, 288, 303

Ear, cochlea, 524
— development of, 635
— eustachian tube of, 523
— external, 519
— labyrinth of, 524
— membrani tympani of, 520
— organ of Corti, 525
— ossicles of the, 522
— semicircular canals of, 525
Ectoderm, 15
Ectomeres, 583
Ectosarc, 62
Efferent nerve, 21, 426
Egg albumin, 39
Eggs as food, 73
Elastic-fibro-cartilage, 29
Elastin, 43
Electric stimulation of muscle, 385
— nerve, 429
Electrodes, non-polarisable, 381
Electrotonus, 433
Elements, 5
Emmetropic eye, 490
Emulsion of fat, 164
Enamel, 78
Endoderm, 15
Endogenous reproduction, 55
Endolymph, 524
Endosarc, 62
Endothelium, development of, 32
— with nitrate of silver, 156
Entomeres, 583
Entoptic images, 494
Epiblast, 12, 16, 584
Epiglottis, 416
Epithelial tissues, 17
Epithelium, 19
— of the tubules of the kidney, 332
Eupnœa, 288
Eustachian tube, 523
Excreting glands, 318
Excretions, 326
Exhaustion, 303
Expiration, 281
External auditory meatus, 520
Eye, abductor nerve of the, 449
— accommodation, 490
— blind spot of, 504
— convergent rays, 488
— development of, 482, 631
— dioptrics of the, 485
— inversion of image by the, 487
— motor occuli nerve, 448
— pigment cells of the retina, 508
— refraction of the, 486
— tunics of the, 478
— yellow spot, 506
Eye-ball, dioptric media of the, 481
Eye-balls, movement of the, 512

Face, develomepnt of, 639
Fæces, composition of, 147
Fallopian tube, 592
Fat, absorption of, 163
Fats as food, 65, 67
Fat cells, 11
— emulsion, 164

Fat of adipose tissue in man, 48
Fats, 48
Fehling's solution, 109
Fenestra ovalis, 524
— rotunda, 524
Fibrin, 176, 178, 200
— chemistry of, 41
— ferment, 178
Fibrinogen, 40
Fibrinoplastin, 178
Fick's spring manometer, 250
Filiform papillæ, 95, 473
Fistula, gastric, 114
— intestinal, 145
— pancreatic, 123
Fœtal circulation, 629
Follicles, lymphatic, 153
— of Lieberkühn, 159
Food, action of gastric juice on, 116
— — of saliva on, 107
— albuminous bodies, 65, 67
— carbohydrates, 65, 67
— chemical composition of, 67
— diet table, 361
— digestibility of, 68
— excessive consumption of, 359
— fats, 65, 67
— mixed diet, 358
— nitrogenous diet, 357
— non-nitrogenous diet, 357
— requirements, 68, 357
— tables, 69
Food-stuffs, 64
— classification of, 66
— ultimate uses of, 360
Fovea centralis, 487
Fungiform papillæ, 95, 473
Fungus cells dividing, 55

Gall bladder, 136, 139
Galvanometer, 382
Ganglion cells of heart, 22
Gases in the blood, 197, 299
— urine, 343
Gastric digestion, 118
— fistula, 114
— glands, 112
— juice, action on food, 116
— juice, artificial, 114
— juice, composition of, 113
— juice, method of obtaining, 114
Gastrula stage, 15
Gelatin, 43
Gemmation, 55
Genito-urinary apparatus, development of, 612
Germinal vesicle, 580
Giddiness, 471
Gills, 270
Gland cells, 96
Glands, acinous, 95
— blood elaborating, 305
— ductless, 306
— excreting, 318
— lachrymal, 318
— lymphatic, 153
— mammary, 321
— Meibomian, 321
— mucous, 97, 319
— of stomach, 112
— salivary, 96
— sebaceous, 320
— secreting, 318
— sudoriferous, 326
— sweat, 326
— thymus, 308
— thyroid, 307
Glandular epithelium, 19
Glisson, capsule of, 130
Globin, 195
Globulins, 40
Glœocapsa, 55
Glomerulus of kidney, 333
Glosso-pharyngeal nerve, 454
Glottis, shape of the opening of the, 417
Glutin, 74
Glycin, 46
Glycocine, 46
Glycocholic acid, 44, 136
Glycocoll, 46
Glycogen, 48
— preparation of, 315
Glycogenic function of liver, 313
Gmelin's test for bile pigments, 136
Goblet-cells, 20, 158
Graafian follicle, 578
Grape sugar, 47
— in the urine, 343
— starch converted into, 108
Graphic method, 392
Gravid uterus, 594
Green vegetables as food, 74

Hæmatin, 194
Hæmatoidin, 195
Hæmin, 195
Hæmochromogen, 194
Hæmoglobin crystals, 192
— decomposition of, 194
— spectra of, 193
Hare lip, 641
Haversian system, 30
Hearing, 516
— external ear, 519
— organ of Corti, 525
Heart, 208
— accelerator nerves of, 231
— action of the valves of, 216
— afferent cardiac nerves, 232
— anabolic action of, 232
— anatomy of, 211
— atropine, curara, digitalis, nicotin, action of, 231
— Bidder's ganglion, 228
— cardiac centre, 557
— cardiac movements, 220
— cardiograph, 222
— capacity of, 213
— cause of sounds of, 224
— cycle of, 218
— diastole of, 219
— depressor nerve, 232
— development of, 621
— extrinsic nerves, 230
— first sound of, 223
— inhibitory nerves of, 230
— innervation of, 225
— intrinsic nerves, 227
— katabolic action, 232
— lymph, 168
— muscle of, 213, 377
— nerve cells of, 22
— passive interval, 220
— second sound of, 224
— semilunar valves, 215
— Stannius's experiment, 229
— systole of, 219
— vagus, action of, 230
— valves of, 215
— work done by the, 261
Heartbeat, nerve mechanism controlling, 228
Heart's impulse, 221
Heat, balance of, 369
— compensation for external variations, 372
Heat, compensation for internal variations, 371
— expenditure of, 368
— income, 367
— regulation, 371
Henle's tubules, 331
Hepatic artery and vein, 131
Hiccough, 292
Hippuric acid, 47
— in the urine, 341
Histology, 1
Holoblastic ovum, 584
Homœothermic animals, 363
Hunger and thirst, 470
Hyaline cartilage, 29
Hydra, neuro-muscular cells of, 20
Hydrocele fluid, 178
Hydrochloric acid in the tissues, 50
Hypermetropia, 493
Hypoblast, 12, 16, 584
Hypoglossal nerve, 457

Idiosyncrasy, 68
Ileo-cæcal valves, 90
Ilium, 77
Incus, 522
Indican, 47, 342
Indifferent cells, 12
Indol, 47, 148
Induced current, 386, 431
Induction coil, 386, 431
Infusoria, 62
Inhibition, 443
Innervation of the heart, 225
Inorganic bodies, 49
— substances, 5
Inosit, 48
Inspiration, 277
Intercellular substance, 11
Intercostal muscles, 279
Interlobular vein, 130
Internal respiration, 300
Interrupted current, 387
Interstitial absorption, 151
Intestinal absorption, 157
— digestion, 146
— fistula, 145
— juice, function of, 145
— — secretion of, 145
— motion, nervous mechanism of, 92
— secretion, method of obtaining, 144

Intestine, histology of small, 89
— large, 147
— lymph follicles, 159
— small, 142
Intestines, movements of the, 88
Intralobular vein, 131
Inversion of image, 487
Iris, 479, 495
— functions of the, 495
— nervous mechanism controlling the, 496

Jejunum, 77
Joints, 408

Karyokinesis, 10
Keratin, 43, 329
Kidney, 330
— blood vessels of, 332
— development of, 616
— relation of blood-vessels to tubules, 334
— tubules of, 331
Krause's end bulbs, 462
Kreatin, 46
Kreatinin, 46
— in the urine, 341
Kymograph, 246

Labyrinth of ear, 524
Lachrymal glands, 318
Lactation, 325
Lacteals, 150, 152, 157, 169
Lactic fermentation, 48
Lactose, 48
Lacunæ of bone, 30
Lakey blood, 189
Larynx, 415
— muscles of, 272
Latent period, 393
Laughing, 292
Lecithin, 5, 44, 137
Leucin, 46
— and tyrosin in the urine, 344
— in pancreatic digestion, 127
Leucocytes, 181
Leucocythemia, 180
Levatores costarum, 279
Levers, the three orders of, 408
Lieberkühn's follicles, 144, 159
Light, 509
Liquor folliculi, 580
— sanguinis, 174
Listing's measurements, 488
Liver, 129
— bile ducts, 134
— bile salts, 44, 136
— capillaries of, 235
— capsule of Glisson, 130
— cells, 9, 132
— development of, 611
— glycogenic function of, 313
— hepatic artery, 132
— interlobular vein, 130
— lobules of, 130
— method of obtaining bile, 135
— portal vein, 314
Ludwig's kymograph, 246
Lumen of cells, 125
Lung bronchial tubes, 273
— development of, 612
— structure of, 271
Lymph and chyle, characters of, 165
— channels, 151
— composition of, 166
— corpuscles, 167
— follicles in intestine, 159
— hearts, 168
— movement of the, 168
— spaces, 151
— vascular system, 151
— vessels, valves in, 169
Lymphatic gland, 152
— system, 151
— vessels, 154
Lymphatics, 150

Making Shock, 430
Malassez' apparatus for the enumeration of blood corpuscles, 188
Malleus, 522
Malpighian body of spleen, 313
— capsule, 330
Mammary glands, 321
— during lactation, 325
Marey's sphymograph, 256
— tambour, 223
Mastication, 78
— nervous mechanism of, 84
Meat as food, 72

Mechanical stimulation of muscle, 385
— of nerve, 429
Mechanism of absorption, 161
Medulla oblongata, as central organ, 553
— as conductor, 552
— cardiac centre, 557
— decussation of fibres in, 552
— pyramids in, 552
— respiratory centre in, 554
— roots of nerves in, 553
— vasa motor centre in, 555
Medullated nerve fibres, 21, 425
Meibomian glands, 321
Meissner's plexus, 93
Membrana tympani, 520
Membrane of Reissner, 525
Membranous spiral lamina, 525
Memory, 570
Menstruation, 580
Meroblastic ovum, 584
Mesoblast, 12, 16, 584
Methæmoglobin, 194
Metabolism, 305
Metazoa, 14
Micrococcus, 57
Micturition, nervous mechanism of, 349
Milk, chemical composition of, 70, 322
— as food, 69
— sugar, 48
— tests, 71
Millon's re-agent, 39
Mitral valve of the heart, 212
Moist chamber, 392
Molecules, 5
Morphology, 1
Morula stage, 15, 583
Motion, application of skeletal muscles, 407
— rate of running, 432
— standing, 410
— walking and running, 413
Motor nerves, 546
— occuli nerve, 448
Mouth, development of, 640
Mouth, digestion, 95
Movement of the chyle, 170
— of the heart, 220
— of the lymph, 168
— of white blood corpuscles, 182
Mucin, 43
Mucous glands, 97, 319
— tissue, 25
Müllerian duct, 613
Murexide test for uric acid, 47
Muscle, active state of, 384
— altitude of curve, 397
— changes during contraction, 387
— chemical change in, 379
— composition of, 379
— consistence of, 378
— contraction of unstriated, 405
— curves, 393
— death rigor, 403
— Du Bois Reymond's coil, 386, 431
— duration of contraction, 395
— effect of temperature on contraction of, 396
— elasticity of, 379
— electric phenomena, 381
— fatigue, 401
— graphic method, 392
— irritability of, 384, 401
— latent period, 393
— maximum contraction, 397
— natural currents, 381
— negative variation, 389
— non-polarisable electrodes, 381
— non-striated, 23, 376
— of heart, 377
— passive state of, 378
— plasma, 37
— properties of, 378
— rate of contractions in insects, 396
— rheoscopic frog, 389
— rigor mortis, 403
— sarcolemma, 24, 377
— single contraction, 393
— stimulation of, 385
— striated, 23, 376
— summation, 398
— tetanus, 398
— tone, 400

Muscle, tracings, 393
— wave of contraction, 394
Muscles of deglutition, 81
— of the eye-balls, 513
— of the iris, 497
— of the larynx, 272, 418
— of mastication, 79
— origin and insertion of, 407
— of respiration, 278
— the three orders of levers, 408
Muscular fibres of heart, 213
Muscularis mucosæ, 143, 159
Myograph, pendulum, 392
— spring, 392
Myopia, 492
Myosin, 40

Nasal ganglion, 453
Native albumins, 39
Nausea, 471
Nerve, 424, 445
— III. motor oculi nerve, 448
— IV. trochlear nerve, 449
— V. trigeminus, or trifacial nerve, 451
— VI. abductor nerve of the eye, 449
— VII. (portio dura) motor nerve of the face, 449
— VIII. vagus, 455
— VIII. glosso-pharyngeal nerve, 454
— VIII. spinal accessory nerve, 454
— IX. hypoglossal nerve, 457
— active state of, 428
— anode, 430
— ascending current, 438
— axis cylinder, 21, 425
— Auerbach's plexus, 92
— breaking shock, 430
— breaking tetanus (Ritter's tetanus), 430
— cathode, 430
— ciliary ganglion, 453
— descending current, 438
— electric change in, 433
— electrical properties of, 428
— electrotonus, 433
— ganglion cells, 22, 447
— irritability of nerve fibres, 435
— law of contraction, 438
— making shock, 430
Nerve, mechanism of heart, 228
— medullary sheath, 21, 426
— medullated fibres, 21, 425
— Meissner's plexus, 93
— multipolar cells, 22
— natural current in, 428
— negative variation, 433
— nerve muscle preparation, 428
— non-medullated fibres, 21, 425
— nodes of Ranvier, 21, 425
— otic ganglion, 454
— polarising current, 434
— primary coil, 431
— primitive sheath, 21, 425
— proximal and distal end, 427
— secondary coil, 431
— sensory cells, 20
— spinal cord, 532
— spinal, 445
— stained with osmic acid, 21, 425
— stimulation of, 429
— submaxillary ganglion, 454
— tissue, 20
— to sphenopalatine ganglion, 453
— velocity of nerve force, 431
Nerves, afferent, 21, 426
— efferent, 21, 426
— anterior roots of, 445
— posterior roots of, 445
— cranial, 448
— functional classification of, 427
Nerve-cells, 22
— functions of, 441
— in spinal cord, 532
Nerve endings, 20, 439
— in the ear, 525
— in the eye, 503
— in nose, 475
— in the skin, 461
— in tongue, 474
Nerve fibre, chemistry of, 427
— fibres in spinal cord, 532
— roots in medulla oblongata, 553
Nervous control of the blood vessels, 267
Nervous mechanism of respiration, 290
— of salivary secretion, 100
— of urinary secretion, 347

Nervous mechanism of voice, 421
Nervous organs, central, 530
Nerve muscle preparation, 428
Neurin, 45
Neuroglia, 425, 530
Neuro-muscular cells of Hydra, 20
Nitrogen in the blood, 198
— in the tissues, 51
Nitrogenous diet, 357
— ingredients in the tissues, 36
Non-medullated nerve-fibres, 21, 425
Non-nitrogenous diet, 357
— ingredients of the body, 47
Non-striated muscle, 23, 376
Nose, development of, 640
— nerve endings in the, 475
Notochord, 584
Nuclear matrix, 10
Nucleus, method of staining, 10
Nucleolus, 10
Nutrition, 352
Nutritive equilibrium, 356
— materials in vegetable food, 74
— value of food, 67

Odontoblasts, 80
Œsophagus, development of, 612
— histology of, 83
Olein, 48
Ophthalmic ganglion, 453
Ophthalmometer, 491
Ophthalmoscope, 498
Optic nerve, 481
— thalami, 552, 566
Organic substances, 5
— substance, instability of, 6
Organisms, chemical composition of, 5
— death of, 7
— general characters of, 4
— reproduction of, 7
— vital characters of, 52
Origin of white blood corpuscles, 183
Osseous spiral lamina, 525
Ossicles of ear, 522
Ossifying cartilage, 31
Osteoblasts, 32
Otic ganglion, 454
Otoliths, 525
Ovary, 579
Ovoid cells of stomach glands, 112
Ovulation, 580
Ovum, 579
— changes in the, 582
— divisions of, 14
Oxalic acid in the urine, 342
Oxygen, 294
— in the blood, 197
— in the tissues, 51
Oxyhæmoglobin, 38, 190, 192, 297
— composition of, 190
— preparation of, 191

Pacinian corpuscles, 463
Pain, 470
Palmitin, 48
Pancreas, 122
— changes in the cells during secretion, 124
— nervous influence on the, 124
— development of, 611
Pancreatic fistula, 123
— juice, action on fat, 128
— — action on proteids, 126
— — action on starch, 128
— — artificial, 123
— — characters of the secretion, 123
Papillæ of tongue, 95, 473
Paraglobulin (fibrinoplastin), 40, 177
Paramœcium 16, 61
Parapeptone, 117
Pavy's solution, 109
Pendulum myograph, Fick's, 392
Peduncles of the cerebrum, 552
Pepsin, 114
Peptic cells, 115
Peptone, 41
— absorption of, 162
— tests for, 42
Perilymph, 524
Peristaltic contraction of intestine, 89
Perspiration, 327
Pettenkofer's test for bile salts, 44, 137
Peyer's patches, 160
Phakoscope, 491
Pharynx, muscles of, 81
Phosphates in the tissues, 50
— in the urine, 343
Physical forces of the circulation, 239
Physiology, objects of, 1
Picric acid test for albumen, 39

Pigment cells, 12
— of the eye, 508
Placenta, 592
— uses of the, 595
Plant cell, 8
Plasma, 174
— chemical composition of, 176
— of the blood, coagulation of, 176
— method of obtaining from blood, 175
Plasmata, 36
Pleura, 271
— functions of the, 282
Pneumogastric nerve, 230, 455
Poikilothermic animals, 363
Poisonous gases, 301
Polarising current, 433
Pons varolii, 552, 564
Portal system, development of, 625
— vein, 130, 314
Portio dura, seventh nerve, 449
— mollis, 516
Porus opticus, 502
Posterior roots of spinal cord, 533
Potassium chloride in the tissues, 50
Potatoes as food, 74
Presbyopia, 493
Primitive grove, 16
Products of tissue change, 42
Protagon, 45
Protamœba, 60
Protista, 14
Protococcus, 59
Protoplasm, 4
— assimilation of, 54
— change in form, 53
— of cell, 9
— in the tissues, 36
— structure of, 10
Protoplasmic movements, 53–4
Protozoa, 14
Pseudopodia of amœba, 53
— of white blood corpuscles, 182
Ptyalin, 108
Puerile breathing, 286
Pulmonary circulation of the blood, 211
Pulp cavity of the teeth, 78
Pupil of the eye, 479
Pulse, 254
— Marey's sphygmograph, 256
— tracings, 256
Pulse, variations in the, 258
Purkinje's cells in the cerebellum, 562
— figures, 505
Putrefactive fermentation in the intestine, 148
Pylorus, 86

Quadratus lumborum, 279

Ranvier's nodes, 21, 425
Receptaculum chyli, 152
Recording apparatus, 245
Rectum, 77
Red blood corpuscles, 174
Reduced hæmoglobin, 192
Reflex action, 21, 442, 542
— inhibition of, 544
Reflex centres, special, 547
Reflexion, 442, 549
Refraction, 485
Reproduction, 577
— of cells, 55, 57
Respiration, 268
— asphyxia, 203
— changes in the air, 294
— changes in the blood during, 296
— chemistry of, 293
— complemental air, 285
— construction of thorax, 273
— diffusion, 286
— expiration, 281
— expired air, 294
— frequency of, 276
— functions of the pleura, 282
— in lower animals, 269
— inspiration, 277
— internal or tissue, 300
— mechanism of, 268
— muscles of, 278
— nervous mechanism of, 286
— of abnormal air, 301
— poisonous gases, 301
— pressure differences in the air, 284
— reserve air, 285
— residual air, 285
— sounds of, 286

Respiration, tidal air, 285
— ventilation, 302
— vital capacity, 285
— vital point, 287
— volume of air, 284
Respiratory centre, 554
— movements, 275
— sounds, 286
— wave, 249
Retention of urine in the bladder, 348
Retina, function of the, 502
— pigment cells of, 508
— ophthalmic view of the, 500
— structure of, 503
Rheoscopic frog, 339
Ribs, 280
Rigor mortis, 403
Ritter's tetanus, 430
Rods and cones of the retina, 503
Rods of Corti, 525

Saccharomyces cerevisiæ, 48—55
Sacculated glands, 95
Sacule of semicircular canals, 525
Saliva, action on food, 107
— chemistry of, 98
— effect of drugs on secretion of, 101
— effect of nervous influence, 101
— method of secretion, 100
Salivary gland, 96
— histology of, 105
Salts as food, 75
Salts in the tissues, 50
Saponification, 128
Sarcolemma of muscle, 24, 377
Scaleni muscles, 279
Scaly epithelium, 19
Scheiner's experiment, 488
Sclerotic, 478
Sebaceous glands, 320
Secreting glands, 318
Secretion, 318
Secretion of urine, 334
Segmentation sphere, 583
Semicircular canals, 525
Semilunar valves, 215
Sensations, general, 470
Sensory nerve cells, 20
Sensory nerves, 546
Serum albumin, 39
— composition of, 179
— globulin, 177
Serum, separation of, 176
Sexual organs, development of, 618
Sexual reproduction, 577
Shivering, 471
Sighing, 292
Sight, 477
Skatol, 148
Skin, cutaneous desquamation, 328
— general sensations, 460, 470
— glands of, 321
— Krause's end bulbs, 462
— nerve endings in, 461
— sense of temperature, 468
Skull, development of, 639
Smell, 475
Sneezing, 292
Sobbing, 292
Sodium chloride in the tissues, 50
Solitary glands, 160
Somatopleure, 585
Sound, 516
— direction of, 529
— tuning forks, 517
— vibrations through the tympanum, 520
Special senses, 458
— hearing, 516
— smell, 475
— taste, 472
— touch, 458
— vision, 477
Spectra of blood, 298
— of hæmoglobin, 192
Spectrum, analysis of the, 510
Speech, 415
Spermatozoa, 578
Sphenopalatine ganglia, 453
Spherical aberration, 494
Spheroidal cells of stomach glands, 112
Sphenograph, 256
Spinal-accessory nerve, 454
Spinal cord, 532
— automatic centres in the, 549
— automatism, 549
— cellular columns in the, 541
— cervical region, 535
— collection of nerve-cell in the, 540
— co-ordination, 548
— course of fibres in, 539
— development of, 599

Spinal cord, dorsal region, 534
— experiments on the, 538
— lumbar region, 534
— motor channels, 546
— of embryo, 536
— pyramidal tracts of, 535
— reflex action, 542
— roots of nerves of, 533
— sensory channels, 546
— white tracts on, 536
Splanchnopleure, 585
Spleen, changes of blood in the, 312
— development of, 611
— extirpation of the, 312
— function of, 311
— structure of, 309
Spring myograph, 392
Standing, 410
Stapes, 522
Starch as food, 74
— converted into grape sugar, 108
— microscopic appearance of, 75
— tests for, 109
Starvation, 353
Steapsin, 146
Stearin, 48
Steno's duct, 98
Stomach, digestion, 111
— histology of, 111
— motion of the, 85
— nervous influence on, 86
— walls of the, 85
Stomata, 156
Stratified epithelium, 18
Striated muscle, 23, 376
Stroma of the blood, 187
— chemistry of the, 195
Submaxillary ganglion, 454
Sudoriferous glands, 326
Sulphates in the tissues, 50
— in the urine, 343
Summation, 398
Supporting tissues, 17
Supra renal capsule, 306
Sweat glands, 326
Symphyses, 408
Syntonin, 40
Systemic circulation of the blood, 211
Systole of heart, 219

Tactile impressions, 465
— sensations, 461
Tambour (Marey's), 223
Taste, 472
Tastebuds, 474
Taurin, 46
Taurocholic acid, 44, 136
Tegmentum, 565
Teeth, development of, 80
— structure of the, 78
Temperature, maintenance of uniform, 369
— measurement of, 364
— normal variations in, 364
Tendon cells stained with gold, 27
Testicle, 578
Tests for albumin, 39
— for peptone, 42
Tetanus of muscle, 398
Thermic stimulation of muscle, 385
— nerve, 429
Thermometer, clinical, 364
Thirst and hunger, 470
Thoracic duct, 150, 169
— lymph of, 166
Thorax, construction of, 273
Thrombosis, 204
Thymus gland, 308
Thyroid body, 307
— cartilage, 416
Timbre of a note, 518
Tissue changes in starvation, 353
— change, products of, 42
— connective, 25
— differentiation, 13
— epithelial, 17
— lymphoid, 153
— mucous, 25
— muscle, 23, 316
— nerve, 20, 425
— white fibrous, 26
— yellow elastic, 27
Tissues, classification of, 17
Titillation, 471
Tones, 518
Tongue, 472
— taste buds of, 474
Torula cerevisiæ, 59
Touch, 461
— cells, 462
— corpuscles (Meissner's), 462
— general sensation, 470
— sense of locality, 464
— sense of pressure, 466
Tradescantia virginica, 52

Tricuspid valve of the heart, 211
Trigeminus nerve, 449
Trochlear nerve, 449
Trommer's test, 109
Trypsin, 125, 146
Tubules of kidney, 331
Tubuli seminiferi, 578
Tunica adventitia, 233
— intima, 235
— granulosa, 580
— media, 233
Tuning forks, 517
Tympanum of ear, 520
Tyrosin, 46
— in pancreatic digestion, 127

Umbilical cord, 595
Unicellular organism, 14
Unstriated muscle, contraction of, 405
Urachus, 591
Urea, 45, 338
— artificial preparation of, 45
— estimation of, 340
— source of, 345
Ureters, 348
Uric acid, 46
— in the urine, 340
— murexide test for, 47
Urinary calculi, 344
Urine, 334
— abnormal constituents in the, 343
— acid fermentation of the, 344
— chemical composition of, 338
— colouring matter of, 342
— inorganic salts in the, 342
— quantity secreted, 335
— retention of, 348
— secretion of, 334
— source of urea, 345
— specific gravity of, 335
Urinary excretion, 330
— secretion, nervous mechanism of, 347
Urobilin, 342
Urochrome, 342
Uroerythrin, 342
Uterus, 577

Vacuoles, 9, 62
Vagus nerve, 230, 455
Vagus stimulation of, 230
Valentine's method, estimating amount of blood, 172
Valsalva's experiment, 523
Valves in lymph vessels, 169
— of heart, 215
— of veins, 237
— of the heart, action of, 216
Valvulæ conventes, 122, 143
Vasa differentia, 578
— motor centre, 555
— motor nerves, 263
Vascular system, development of 32, 619
Vegetable cells, 8
— food, 73
Veins, coats of, 236
— valves of, 237
Velocity of the blood current, 259
Venæ advehentes, 625
Vena cava, 211
— porta, 314
Venous system, development of, 629
Ventilation, 302
Ventricles of brain, 552
— of heart, 211
Vesiculæ seminalis, 578
Vessels, lymphatic, 154
Vibration, 517
Villi, 143
— lacteals in, 157
Vision, 477
— accommodation, 490
— astigmatism, 494
— binocular, 514
— chromatic aberration, 493
— colour blindness, 511
— colour perceptions, 509
— complementary colours, 510
— conditions affecting, 507
— convergent rays, 488
— entoptic images, 494
— function of the retina, 502
— hypermetropia, 493
— irradiation, 507
— judgment of distance, 514
— judgment of size, 514
— light impressions, 501
— mental operations in, 512
— myopia, 492
— negative after image, 507
— ophthalmoscope, 498
— positive after image, 507
— presbyopia, 493

Vision, Purkinje's figures, 505
— refraction, 485
— retinal stimulation, 506
— Scheiner's experiment, 488
— spherical aberration, 494
Vital capacity, 285
— characters of organisms, 52
— phenomena, 2, 7
— point, 287
Vitellin, 40
Vitelline membrane, 580
Vitreous humour, 479
Vocal cords, 416
Voice and speech, 415
— nervous mechanism of, 421
— properties of the human, 420
Volition, 549
Vomiting, 86
Vorticella, 16, 63

Walking and running, 413
Warm-blooded animals, 363
Waste products of animal body, 45
Water H_2O, 6, 49
Water as food, 75
Weber's method, estimating amount of blood, 172
Welcker's method, estimating amount of blood, 173
Wharton's duct, 98
White blood corpuscles, 181
— fibro-cartilage, 29
— fibrous tissue, 26
— substance of Schwann, 426
Wolffian bodies, 613

Xanthin in the urine, 341
Xanthoproteic test, 39

Yawning, 292
Yeast plant, 48, 55, 59
Yellow elastic tissue, 27
— spot, 506
Yolk of egg, 581
— sac, 589

Zona pellucida, 580
— tendinosa, 213
Zymogen, 126

WELLCOME LIBRARY INSTITUTE

BRADBURY, AGNEW, & CO., PRINTERS, WHITEFRIARS.

LONDON, *February*, 1889.

J. & A. CHURCHILL'S

MEDICAL CLASS BOOKS.

ANATOMY.

BRAUNE.—**An Atlas of Topographical Anatomy**, after Plane Sections of Frozen Bodies. By WILHELM BRAUNE, Professor of Anatomy in the University of Leipzig. Translated by EDWARD BELLAMY, F.R.C.S., Surgeon to Charing Cross Hospital, and Lecturer on Surgery in its School. With 34 Photo-lithographic Plates and 46 Woodcuts. Large Imp. 8vo, 40s.

FLOWER.—**Diagrams of the Nerves of the Human Body**, exhibiting their Origin, Divisions, and Connexions, with their Distribution to the various Regions of the Cutaneous Surface, and to all the Muscles. By WILLIAM H. FLOWER, C.B., F.R.C.S., F.R.S. Third Edition, containing 6 Plates. Royal 4to, 12s.

GODLEE.—**An Atlas of Human Anatomy:** illustrating most of the ordinary Dissections and many not usually practised by the Student. By RICKMAN J. GODLEE, M.S., F.R.C.S., Surgeon to University College Hospital; Teacher of Operative Surgery, and Assistant Professor of Clinical Surgery in University College; With 48 Imp. 4to Coloured Plates, containing 112 Figures, and a Volume of Explanatory Text, with many Engravings. 8vo, £4 14s. 6d.

HEATH.—**Practical Anatomy: a Manual of Dissections.** By CHRISTOPHER HEATH, F.R.C.S., Holme Professor of Clinical Surgery in University College and Surgeon to the Hospital. Seventh Edition, revised by RICKMAN J. GODLEE, M.S. Lond., F.R.C.S., Teacher of Operative Surgery, and Assistant Professor of Clinical Surgery in University College, and Surgeon to the Hospital. With 24 Coloured Plates and 278 Engravings. Crown 8vo, 15s.

ANATOMY—*continued.*

HOLDEN.—**A Manual of the Dissection of the** Human Body. By LUTHER HOLDEN, F.R.C.S., Consulting-Surgeon to St. Bartholomew's Hospital. Fifth Edition, by JOHN LANGTON, F.R.C.S., Surgeon to, and Lecturer on Anatomy at, St. Bartholomew's Hospital. With 208 Engravings. 8vo, 20s.

By the same Author.

Human Osteology: comprising a Description of the Bones, with Delineations of the Attachments of the Muscles, the General and Microscopical Structure of Bone and its Development. Seventh Edition, edited by CHARLES STEWART, Conservator of the Museum and Hunterian Professor of Comparative Anatomy and Physiology, R.C.S., and R. W. REID, M.D., F.R.C.S., Lecturer on Anatomy at St. Thomas's Hospital, Examiner in Osteology to the Conjoint Examining Board, R.C.P. Lond. and R.C.S. Eng. With 59 Lithographic Plates and 75 Engravings. Royal 8vo, 16s.

ALSO,

Landmarks, Medical and Surgical. Fourth Edition. 8vo, 3s. 6d.

MORRIS.—**The Anatomy of the Joints of Man.** By HENRY MORRIS, M.A., F.R.C.S., Surgeon to, and Lecturer on Anatomy and Practical Surgery at, the Middlesex Hospital. With 44 Plates (19 Coloured) and Engravings. 8vo, 16s.

The Anatomical Remembrancer; or, Complete Pocket Anatomist. Eighth Edition. 32mo, 3s. 6d.

WAGSTAFFE.—**The Student's Guide to Human** Osteology. By WM. WARWICK WAGSTAFFE, F.R.C.S., late Assistant-Surgeon to, and Lecturer on Anatomy at, St. Thomas's Hospital. With 23 Plates and 66 Engravings. Fcap. 8vo, 10s. 6d.

WILSON — BUCHANAN — CLARK. — **Wilson's** Anatomist's Vade-Mecum: a System of Human Anatomy. Tenth Edition, by GEORGE BUCHANAN, Professor of Clinical Surgery in the University of Glasgow, and HENRY E. CLARK, M.R.C.S., Lecturer on Anatomy in the Glasgow Royal Infirmary School of Medicine. With 450 Engravings, including 26 Coloured Plates. Crown 8vo, 18s.

BOTANY.

BENTLEY AND TRIMEN.—**Medicinal Plants:** being descriptions, with original Figures, of the Principal Plants employed in Medicine, and an account of their Properties and Uses. By ROBERT BENTLEY, F.L.S., and HENRY TRIMEN, M.B., F.R.S., F.L.S. In 4 Vols., large 8vo, with 306 Coloured Plates, bound in half morocco, gilt edges, £11 11s.

BENTLEY.—**A Manual of Botany.** By Robert BENTLEY, F.L.S., M.R.C.S., late Professor of Botany in King's College and to the Pharmaceutical Society. With nearly 1178 Engravings. Fifth Edition. Crown 8vo, 15s.

By the same Author.

The Student's Guide to Structural, Morphological, and Physiological Botany. With 660 Engravings. Fcap. 8vo, 7s. 6d.

ALSO,

The Student's Guide to Systematic Botany, including the Classification of Plants and Descriptive Botany. With 357 Engravings. Fcap. 8vo, 3s. 6d.

CHEMISTRY.

BLOXAM.—**Chemistry, Inorganic and Organic;** with Experiments. By CHARLES L. BLOXAM, late Professor of Chemistry in King's College. Sixth Edition. With 288 Illustrations. 8vo, 18s.

By the same Author.

Laboratory Teaching; or, Progressive Exercises in Practical Chemistry. Fifth Edition. With 89 Engravings. Crown 8vo, 5s. 6d.

BOWMAN AND BLOXAM.—**Practical Chemistry,** including Analysis. By JOHN E. BOWMAN, and CHARLES L. BLOXAM, late Professor of Chemistry in King's College. Eighth Edition. With 90 Engravings. Fcap. 8vo, 5s. 6d.

CLOWES.—**Practical Chemistry and Qualitative Inorganic Analysis.** Adapted for use in the Laboratories of Schools and Colleges. By FRANK CLOWES, D.Sc. Lond., Professor of Chemistry in University College, Nottingham. Fourth Edition. With Engravings. Post 8vo, 7s. 6d.

CHEMISTRY—*continued.*

COOK.—**Introductory Inorganic Analysis.** A First Course of Chemical Testing. By ERNEST H. COOK, D.Sc. Lond., F.C.S., Physical Science Master, Merchant Venturers' School, Bristol. Crown 8vo, 1s. 6d.

FOWNES.—**Manual of Chemistry.**—*See WATTS.*

FRANKLAND AND JAPP.—**Inorganic Chemistry.** By EDWARD FRANKLAND, Ph.D., D.C.L., F.R.S., and F. R. JAPP, M.A., Ph.D., F.I.C. With 2 Lithographic Plates and numerous Wood Engravings. 8vo, 24s.

JOHNSON.—**The Analyst's Laboratory Companion.** By ALFRED E. JOHNSON, Assoc. R.C.Sc.I., F.I.C., F.C.S., First Prizeman in Chemistry, Physics, and Mathematics of R.C.Sc.I. Crown 8vo, 5s.

MORLEY.—**Outlines of Organic Chemistry.** By H. FORSTER MORLEY, M.A., D.Sc., Joint Editor of "Watts' Dictionary of Chemistry." Crown 8vo, 7s. 6d.

VACHER.—**A Primer of Chemistry, including Analysis.** By ARTHUR VACHER. 18mo, 1s.

VALENTIN.—**Chemical Tables for the Lecture-room and Laboratory.** By WILLIAM G. VALENTIN, F.C.S. In Five large Sheets, 5s. 6d.

VALENTIN AND HODGKINSON.—**A Course of Qualitative Chemical Analysis.** By the late W. G. VALENTIN, F.C.S. Seventh Edition by Dr. W. R. HODGKINSON, F.R.S.E., Professor of Chemistry and Physics in the Royal Artillery College, and Royal Military Academy, Woolwich; assisted by H. CHAPMAN-JONES, F.C.S., Demonstrator in the Royal School of Mines, and F. E. MATTHEWS, Ph.D., of Cooper's Hill College. With Engravings and Map of Spectra. 8vo, 8s. 6d.

The Tables for the Qualitative Analysis of Simple and Compound Substances, with Map of Spectra, printed separately. 8vo, 2s. 6d.

CHEMISTRY—*continued.*

WATTS.—**Physical and Inorganic Chemistry.**

By HENRY WATTS, B.A., F.R.S. (being Vol. I. of the Thirteenth Edition of Fownes' Manual of Chemistry). With 150 Wood Engravings, and Coloured Plate of Spectra. Crown 8vo, 9s.

By the same Author.

Chemistry of Carbon-Compounds, or Organic Chemistry (being Vol. II. of the Thirteenth Edition of Fownes' Manual of Chemistry). Edited by WM. A. TILDEN, D.Sc., F.R.S. With Engravings. Crown 8vo, 10s.

CHILDREN, DISEASES OF.

DAY.—**A Manual of the Diseases of Children.**

By WILLIAM H. DAY, M.D., Physician to the Samaritan Hospital for Women and Children. Second Edition. Crown 8vo, 12s. 6d.

ELLIS.—**A Practical Manual of the Diseases** of Children. By EDWARD ELLIS, M.D., late Senior Physician to the Victoria Hospital for Sick Children. With a Formulary. Fifth Edition. Crown 8vo, 10s.

GOODHART.—**The Student's Guide to Diseases** of Children. By JAMES FREDERIC GOODHART, M.D., F.R.C.P., Physician to Guy's Hospital and Lecturer on Pathology in its Medical School; Physician to the Evelina Hospital for Sick Children. Third Edition. Fcap. 8vo, 10s. 6d.

SMITH.—**On the Wasting Diseases of Infants** and Children. By EUSTACE SMITH, M.D., F.R.C.P., Physician to H.M. the King of the Belgians, and to the East London Hospital for Children. Fifth Edition. Post 8vo, 8s. 6d.

By the same Author.

A Practical Treatise on Disease in Children. 8vo, 22s.

Also,

Clinical Studies of Disease in Children. Second Edition. Post 8vo, 7s. 6d.

STEINER.—**Compendium of Children's Diseases;** a Handbook for Practitioners and Students. By JOHANN STEINER, M.D. Translated by LAWSON TAIT, F.R.C.S., Surgeon to the Birmingham Hospital for Women, &c. 8vo, 12s. 6d.

DENTISTRY.

HARRIS. — **The Principles and Practice of** Dentistry; including Anatomy, Physiology, Pathology, Therapeutics, Dental Surgery, and Mechanism. By CHAPIN A. HARRIS, M.D., D.D.S. Eleventh Edition, revised and edited by FERDINAND J. S. GORGAS, A.M., M.D., D.D.S. With 750 Illustrations. 8vo, 31s. 6d.

SEWILL.—**The Student's Guide to Dental** Anatomy and Surgery. By HENRY E. SEWILL, M.R.C.S., L.D.S., late Dental Surgeon to the West London Hospital. Second Edition. With 78 Engravings. Fcap. 8vo, 5s. 6d.

STOCKEN.—**Elements of Dental Materia Medica** and Therapeutics, with Pharmacopœia. By JAMES STOCKEN, L.D.S.R.C.S., late Lecturer on Dental Materia Medica and Therapeutics and Dental Surgeon to the National Dental Hospital; assisted by THOMAS GADDES, L.D.S. Eng. and Edin. Third Edition. Fcap. 8vo, 7s. 6d.

TOMES (C. S.).—**Manual of Dental Anatomy,** Human and Comparative. By CHARLES S. TOMES, M.A., F.R.S. Third Edition. With 200 Engravings. Crown 8vo. (*In the Press.*)

TOMES (J. and C. S.).—**A System of Dental** Surgery. By Sir JOHN TOMES, F.R.S., and CHARLES S. TOMES, M.A., M.R.C.S., F.R.S.; late Lecturer on Anatomy and Physiology to the Dental Hospital of London. Third Edition. With 292 Engravings. Crown 8vo, 15s.

EAR, DISEASES OF.

BURNETT.—**The Ear: its Anatomy, Physio-** logy, and Diseases. A Practical Treatise for the Use of Medical Students and Practitioners. By CHARLES H. BURNETT, M.D., Aural Surgeon to the Presbyterian Hospital, Philadelphia. Second Edition. With 107 Engravings. 8vo, 18s.

DALBY.—**On Diseases and Injuries of the Ear.** By Sir WILLIAM B. DALBY, F.R.C.S., Aural Surgeon to, and Lecturer on Aural Surgery at, St. George's Hospital. Third Edition. With Engravings. Crown 8vo. 7s. 6d.

EAR, DISEASES OF—*continued.*

JONES.—**Practitioner's Handbook of Diseases** of the Ear and Naso-Pharynx. By H. MACNAUGHTON JONES, M.D., M.Ch.; Examiner, and late Professor in the Queen's University; and Surgeon to the Cork Ophthalmic and Aural Hospital. Third Edition of "Aural Surgery." With 128 Engravings, and 2 Coloured Plates (16 Figures). Royal 8vo, 6s.

By the same Author.

Atlas of the Diseases of the Membrana Tympani. In Coloured Plates, containing 59 Figures. With Explanatory Text. Crown 4to, 21s.

FORENSIC MEDICINE.

ABERCROMBIE. — **The Student's Guide to** Medical Jurisprudence. By JOHN ABERCROMBIE, M.D., F.R.C.P. Senior Assistant Physician to, and Lecturer on Forensic Medicine at, Charing Cross Hospital. Fcap. 8vo, 7s. 6d.

OGSTON.—**Lectures on Medical Jurisprudence.** By FRANCIS OGSTON, M.D., late Professor of Medical Jurisprudence and Medical Logic in the University of Aberdeen. Edited by FRANCIS OGSTON, Jun., M.D., late Lecturer on Practical Toxicology in the University of Aberdeen. With 12 Plates. 8vo, 18s.

TAYLOR.—**The Principles and Practice of** Medical Jurisprudence. By ALFRED S. TAYLOR, M.D., F.R.S. Third Edition, revised by THOMAS STEVENSON, M.D., F.R.C.P., Lecturer on Chemistry and Medical Jurisprudence at Guy's Hospital; Examiner in Chemistry at the Royal College of Physicians; Official Analyst to the Home Office. With 188 Engravings. 2 Vols. 8vo, 31s. 6d.

By the same Author.

A Manual of Medical Jurisprudence. Eleventh Edition, revised by THOMAS STEVENSON, M.D., F.R.C.P. With 56 Engravings. Crown 8vo, 14s.

ALSO,

On Poisons, in relation to Medical Jurisprudence and Medicine. Third Edition. With 104 Engravings. Crown 8vo, 16s.

TIDY AND WOODMAN.—**A Handy-Book of** Forensic Medicine and Toxicology. By C. MEYMOTT TIDY, M.B.; and W. BATHURST WOODMAN, M.D., F.R.C.P. With 8 Lithographic Plates and 116 Wood Engravings. 8vo, 31s. 6d.

HYGIENE.

PARKES.—**A Manual of Practical Hygiene.** By EDMUND A. PARKES, M.D., F.R.S. Seventh Edition by F. DE CHAUMONT, M.D., F.R.S., late Professor of Military Hygiene in the Army Medical School. With 9 Plates and 101 Engravings. 8vo, 18s.

WILSON.—**A Handbook of Hygiene and Sanitary Science.** By GEORGE WILSON, M.A., M.D., F.R.S.E., Medical Officer of Health for Mid Warwickshire. Sixth Edition. With Engravings. Crown 8vo, 10s. 6d.

MATERIA MEDICA AND THERAPEUTICS.

LESCHER.—**Recent Materia Medica. Notes** on their Origin and Therapeutics. By F. HARWOOD LESCHER, F.C.S., Pereira Medallist. Third Edition. 8vo, 2s. 6d.

OWEN.—**A Manual of Materia Medica; incorporating** the Author's "Tables of Materia Medica." By ISAMBARD OWEN, M.D., F.R.C.P., Lecturer on Materia Medica and Therapeutics to St. George's Hospital. Second Edition. Crown 8vo, 6s. 6d.

ROYLE AND HARLEY.—**A Manual of Materia** Medica and Therapeutics. By J. FORBES ROYLE, M.D., F.R.S., and JOHN HARLEY, M.D., F.R.C.P., Physician to, and Joint Lecturer on Clinical Medicine at, St. Thomas's Hospital. Sixth Edition, including addition and alterations in the B.P. 1885. With 139 Engravings. Crown 8vo, 15s.

SOUTHALL.—**The Organic Materia Medica of** the British Pharmacopœia, Systematically Arranged. By W. SOUTHALL. F.L.S. Fourth Edition. Crown 8vo, 5s.

THOROWGOOD.—**The Student's Guide to** Materia Medica and Therapeutics. By JOHN C. THOROWGOOD, M.D., F.R.C.P., Lecturer on Materia Medica at the Middlesex Hospital. Second Edition. With Engravings. Fcap. 8vo, 7s.

WARING.—**A Manual of Practical Therapeu-** tics. By EDWARD J. WARING, C.I.E., M.D., F.R.C.P. Fourth Edition, revised by the Author and DUDLEY W. BUXTON, M.D., M.R.C.P. Crown 8vo, 14s.

MEDICINE.

BARCLAY.—A Manual of Medical Diagnosis. By A. WHYTE BARCLAY, M.D., F.R.C.P., late Physician to, and Lecturer on Medicine at, St. George's Hospital. Third Edition. Fcap. 8vo, 10s. 6d.

CHARTERIS.—The Student's Guide to the Practice of Medicine. By M. CHARTERIS, M.D., Professor of Therapeutics and Materia Medica, University of Glasgow. With Engravings on Copper and Wood. Fifth Edition. Fcap. 8vo, 9s.

FAGGE.—The Principles and Practice of Medicine. By the late C. HILTON FAGGE, M.D., F.R.C.P., Edited by PHILIP H. PYE-SMITH, M.D., F.R.S., F.R.C.P., Physician to, and Lecturer on Medicine in, Guy's Hospital. Second Edition. 2 Vols. 8vo. Cloth, 38s., leather, 44s.

FENWICK.—The Student's Guide to Medical Diagnosis. By SAMUEL FENWICK, M.D., F.R.C.P., Physician to the London Hospital. Sixth Edition. With 114 Engravings. Fcap. 8vo, 7s.

By the same Author.

The Student's Outlines of Medical Treatment. Second Edition. Fcap. 8vo, 7s.

HARRIS.—The Student's Guide to Diseases of the Chest. By VINCENT D. HARRIS, M.D., F.R.C.P., Physician to the Victoria Park Hospital for Diseases of the Chest. With 55 Engravings, plain and Coloured. Fcap. 8vo, 7s. 6d.

WARNER.—The Student's Guide to Clinical Medicine and Case-Taking. By FRANCIS WARNER, M.D., F.R.C.P., Physician to the London Hospital. Second Edition. Fcap. 8vo, 5s.

WEST.—How to Examine the Chest: being a Practical Guide for the Use of Students. By SAMUEL WEST, M.D., F.R.C.P., Assistant Physician to St. Bartholomew's Hospital, Physician to the City of London Hospital for Diseases of the Chest, &c. With 42 Engravings. Fcap. 8vo, 5s.

WHITTAKER.—Student's Primer on the Urine. By J. TRAVIS WHITTAKER, M.D., Clinical Demonstrator at the Royal Infirmary, Glasgow. With Illustrations, and 16 Plates etched on Copper. Post 8vo, 4s. 6d.

MIDWIFERY.

BARNES.—**Lectures on Obstetric Operations,** including the Treatment of Hæmorrhage, and forming a Guide to the Management of Difficult Labour. By ROBERT BARNES, M.D., F.R.C.P., Consulting Obstetric Physician to St. George's Hospital. Fourth (and cheaper) Edition. With 121 Engravings. 8vo, 12s. 6d.

BURTON.—**Handbook of Midwifery for Mid-**wives. By JOHN E. BURTON, M.R.C.S., L.R.C.P., Surgeon to the Liverpool Hospital for Women. Second Edition. With Engravings. Fcap 8vo, 6s.

GALABIN.—**A Manual of Midwifery. By Alfred** LEWIS GALABIN, M.A., M.D., F.R.C.P., Obstetric Physician and Lecturer on Midwifery, &c., to Guy's Hospital, Examiner in Midwifery to the Conjoint Examining Board for England. With 227 Engravings. Crown 8vo, 15s.

RAMSBOTHAM.—**The Principles and Practice** of Obstetric Medicine and Surgery. By FRANCIS H. RAMSBOTHAM, M.D., formerly Obstetric Physician to the London Hospital. Fifth Edition. With 120 Plates, forming one thick handsome volume. 8vo, 22s.

REYNOLDS.—**Notes on Midwifery: specially** designed to assist the Student in preparing for Examination. By J. J. REYNOLDS, L.R.C.P., M.R.C.S. Second Edition. With 15 Engravings. Fcap. 8vo, 4s.

ROBERTS.—**The Student's Guide to the Practice** of Midwifery. By D. LLOYD ROBERTS, M.D., F.R.C.P., Lecturer on Clinical Midwifery and Diseases of Women at Owen's College, Physician to St. Mary's Hospital, Manchester. Third Edition. With 2 Coloured Plates and 127 Engravings. Fcap. 8vo, 7s. 6d.

SCHROEDER.—**A Manual of Midwifery; includ-**ing the Pathology of Pregnancy and the Puerperal State. By KARL SCHROEDER, M.D., Professor of Midwifery in the University of Erlangen. Translated by C. H. CARTER, M.D. With Engravings. 8vo, 12s. 6d.

SWAYNE.—**Obstetric Aphorisms for the Use of** Students commencing Midwifery Practice. By JOSEPH G. SWAYNE, M.D., Lecturer on Obstetric Medicine at the Bristol Medical School. Ninth Edition. With 17 Engravings. Fcap. 8vo, 3s. 6d.

MICROSCOPY.

CARPENTER.—The Microscope and its Revelations. By WILLIAM B. CARPENTER, C.B., M.D., F.R.S. Seventh Edition. With about 600 Engravings. Crown 8vo. (*Preparing.*)

LEE. — The Microtomist's Vade-Mecum; a Handbook of the Methods of Microscopic Anatomy. By ARTHUR BOLLES LEE. Crown 8vo, 8s. 6d.

MARSH. — Microscopical Section-Cutting: a Practical Guide to the Preparation and Mounting of Sections for the Microscope. By Dr. SYLVESTER MARSH. Second Edition. With 17 Engravings. Fcap. 8vo, 3s. 6d.

MARTIN.—A Manual of Microscopic Mounting. By J. H. MARTIN. Second Edition. With Plates and Wood Engravings. 8vo, 7s. 6d.

OPHTHALMOLOGY.

HARTRIDGE.—The Refraction of the Eye. By GUSTAVUS HARTRIDGE, F.R.C.S., Surgeon to the Royal Westminster Ophthalmic Hospital. Second Edition. With 94 Illustrations, Test Types, &c. Crown 8vo, 5s. 6d.

HIGGENS.—Hints on Ophthalmic Out-Patient Practice. By CHARLES HIGGENS, F.R.C.S., Ophthalmic Surgeon to, and Lecture on Ophthalmology at, Guy's Hospital. Third Edition. Fcap. 8vo, 3s.

MACNAMARA.—A Manual of the Diseases of the Eye. By CHARLES MACNAMARA, F.R.C.S., Surgeon to, and Lecturer on Surgery at, the Westminster Hospital. Fourth Edition. With 4 Coloured Plates and 66 Engravings. Crown 8vo, 10s. 6d.

NETTLESHIP.—The Student's Guide to Diseases of the Eye. By EDWARD NETTLESHIP, F.R.C.S., Ophthalmic Surgeon to, and Lecturer on Ophthalmic Surgery at, St. Thomas's Hospital. Fourth Edition. With 164 Engravings, and a Set of Coloured Papers illustrating Colour-blindness. Fcap. 8vo, 7s. 6d.

POLLOCK.—The Normal and Pathological Histology of the Human Eye and Eyelids. By C. FRED. POLLOCK, M.D., F.R.C.S.E., and F.R.S.E., Surgeon for Diseases of the Eye, Anderson's College Dispensary, Glasgow. With 100 Plates, containing 230 Original Drawings by the Author, Lithographed in black and colours. Crown 8vo, 15s.

OPHTHALMOLOGY—*continued.*

WOLFE.—**On Diseases and Injuries of the Eye:** a Course of Systematic and Clinical Lectures to Students and Medical Practitioners. By J. R. WOLFE, M.D., F.R.C.S.E., Senior Surgeon to the Glasgow Ophthalmic Institution, Lecturer on Ophthalmic Medicine and Surgery in Anderson's College. With 10 Coloured Plates, and 120 Wood Engravings, 8vo, 21s.

PATHOLOGY.

BOWLBY.—**The Student's Guide to Surgical** Pathology and Morbid Anatomy. By ANTHONY A. BOWLBY, F.R.C.S., Surgical Registrar and Demonstrator of Surgical Pathology at St. Bartholomew's Hospital. With 135 Engravings. Fcap. 8vo, 9s.

JONES AND SIEVEKING.—**A Manual of Pathological** Anatomy. By C. HANDFIELD JONES, M.B., F.R.S., and EDWARD H. SIEVEKING M.D., F.R.C.P. Second Edition. Edited, with considerable enlargement, by J. F. PAYNE, M.B., Assistant-Physician and Lecturer on General Pathology at St. Thomas's Hospital. With 195 Engravings. Crown 8vo, 16s.

LANCEREAUX.—**Atlas of Pathological Anatomy.** By Dr. LANCEREAUX. Translated by W. S. GREENFIELD, M.D., Professor of Pathology in the University of Edinburgh. With 70 Coloured Plates. Imperial 8vo, £5 5s.

SUTTON.—**An Introduction to General** Pathology. By JOHN BLAND SUTTON, F.R.C.S., Sir E. WILSON Lecturer on Pathology, R.C.S.; Assistant Surgeon to, and Lecturer on Anatomy at, Middlesex Hospital. With 149 Engravings. 8vo, 14s.

VIRCHOW.—**Post-Mortem Examinations:** a Description and Explanation of the Method of Performing them, with especial reference to Medico-Legal Practice. By Professor RUDOLPH VIRCHOW, Berlin Charité Hospital. Translated by Dr. T. B. SMITH. Second Edition, with 4 Plates. Fcap. 8vo, 3s. 6d.

PHYSICS.

DRAPER.—**A Text Book of Medical Physics,** for the use of Students and Practitioners of Medicine By JOHN C. DRAPER, M.D., LL.D., Professor of Chemistry and Physics in the University of New York. With 377 Engravings. 8vo, 18s.

PHYSIOLOGY.

CARPENTER.—**Principles of Human Physiology.** By WILLIAM B. CARPENTER, C.B., M.D., F.R.S. Ninth Edition. Edited by Henry Power, M.B., F.R.C.S. With 3 Steel Plates and 377 Wood Engravings. 8vo, 31s. 6d.

DALTON.—**A Treatise on Human Physiology:** designed for the use of Students and Practitioners of Medicine. By JOHN C. DALTON, M.D., Professor of Physiology and Hygiene in the College of Physicians and Surgeons, New York. Seventh Edition. With 252 Engravings. Royal 8vo, 20s.

FREY.—**The Histology and Histo-Chemistry of Man.** A Treatise on the Elements of Composition and Structure of the Human Body. By HEINRICH FREY, Professor of Medicine in Zurich. Translated by ARTHUR E. BARKER, Assistant-Surgeon to the University College Hospital. With 608 Engravings. 8vo, 21s.

SANDERSON.—**Handbook for the Physiological Laboratory:** containing an Exposition of the fundamental facts of the Science, with explicit Directions for their demonstration. By J. BURDON SANDERSON, M.D., F.R.S.; E. KLEIN, M.D., F.R.S.; MICHAEL FOSTER, M.D., F.R.S., and T. LAUDER BRUNTON, M.D., F.R.S. 2 Vols., with 123 Plates. 8vo, 24s.

SHORE.—**Elementary Practical Biology. Vegetable.** By THOMAS W. SHORE, M.D., B.Sc. Lond., Lecturer on Comparative Anatomy at St. Bartholomew's Hospital. 8vo, 6s.

YEO.—**A Manual of Physiology for the Use of Junior Students of Medicine.** By GERALD F. YEO, M.D., F.R.C.S. Professor of Physiology in King's College, London. Second Edition. With 318 Engravings (many figures). Crown 8vo, 14s.

PSYCHOLOGY.

BUCKNILL AND TUKE.—**A Manual of Psychological Medicine:** containing the Lunacy Laws, Nosology, Ætiology, Statistics, Description, Diagnosis, Pathology, and Treatment of Insanity, with an Appendix of Cases. By JOHN C. BUCKNILL, M.D. F.R.S., and D. HACK TUKE, M.D., F.R.C.P. Fourth Edition with 12 Plates (30 Figures). 8vo, 25s.

CLOUSTON.—**Clinical Lectures on Mental Diseases.** By THOMAS S. CLOUSTON, M.D., and F.R.C.P. Edin.; Lecturer on Mental Diseases in the University of Edinburgh. Second Edition. With 8 Plates (6 Coloured). Crown 8vo, 12s. 6d.

SURGERY.

BELLAMY.—The Student's Guide to Surgical Anatomy; an Introduction to Operative Surgery. By EDWARD BELLAMY, F.R.C.S., Surgeon to, and Lecturer on Surgery at, Charing Cross Hospital. Third Edition. With 80 Engravings. Fcap. 8vo, 7s. 6d.

BRYANT.—A Manual for the Practice of Surgery. By THOMAS BRYANT, F.R.C.S., Consulting Surgeon to Guy's Hospital. Fourth Edition. With 750 Illustrations (many being coloured), and including 6 Chromo-Lithographic Plates. 2 Vols. Crown 8vo, 32s.

DRUITT AND BOYD.—Druitt's Surgeon's Vade-Mecum; a Manual of Modern Surgery. Edited by STANLEY BOYD, M.B., B.S. Lond., F.R.C.S., Assistant Surgeon and Pathologist to the Charing Cross Hospital. Twelfth Edition. With 373 Engravings. Crown 8vo, 16s.

HEATH.—A Manual of Minor Surgery and Bandaging. By CHRISTOPHER HEATH, F.R.C.S., Holme Professor of Clinical Surgery in University College and Surgeon to the Hospital. Eighth Edition. With 142 Engravings. Fcap. 8vo, 6s.

By the same Author.

A Course of Operative Surgery: with Twenty Plates (containing many figures) drawn from Nature by M. LÉVEILLÉ, and Coloured. Second Edition. Large 8vo, 30s.

ALSO,

The Student's Guide to Surgical Diagnosis. Second Edition. Fcap. 8vo, 6s. 6d.

JACOBSON.—The Operations of Surgery: intended especially for the use of those recently appointed on a Hospital Staff, and for those preparing for the Higher Examinations. By W. H. A. JACOBSON, M.A., M.B., M.Ch. Oxon., F.R.C.S., Assistant Surgeon to Guy's Hospital, Teacher of Operative Surgery and Joint Teacher of Practical Surgery in the Medical School. With 199 Engravings. 8vo, 30s.

SURGERY—*continued.*

SOUTHAM.—**Regional Surgery: including Surgical Diagnosis.** A Manual for the use of Students. By FREDERICK A. SOUTHAM, M.A., M.B. Oxon., F.R.C.S., Assistant-Surgeon to the Royal Infirmary, and Assistant-Lecturer on Surgery in the Owen's College School of Medicine, Manchester. Vol. 2. The Upper Extremity and Thorax. Crown 8vo, 7s. 6d. Vol. 3. The Abdomen and Lower Extremity. Crown 8vo, 7s.

WALSHAM.—**Surgery: its Theory and Practice** (Student's Guide Series). By WILLIAM J. WALSHAM, F.R.C.S., Assistant Surgeon to St. Bartholomew's Hospital. Second Edition. With Engravings. Fcap. 8vo. (*In the Press.*)

TERMINOLOGY.

DUNGLISON.—**Medical Lexicon: a Dictionary** of Medical Science, containing a concise Explanation of its various Subjects and Terms, with Accentuation, Etymology, Synonyms, &c. New Edition, thoroughly revised by RICHARD J. DUNGLISON, M.D. Royal 8vo, 28s.

MAYNE.—**A Medical Vocabulary: being an** Explanation of all Terms and Phrases used in the various Departments of Medical Science and Practice, giving their Derivation, Meaning, Application, and Pronunciation. By R. G. MAYNE, M.D., LL.D. Sixth Edition, by W. W. WAGSTAFFE, B.A., F.R.C.S. Crown 8vo, 10s. 6d.

WOMEN, DISEASES OF.

BARNES.—**A Clinical History of the Medical** and Surgical Diseases of Women. By ROBERT BARNES, M.D., F.R.C.P., Obstetric Physician to, and Lecturer on Diseases of Women, &c., at, St. George's Hospital. Second Edition. With 181 Engravings. 8vo, 28s.

BYFORD.—**The Practice of Medicine and** Surgery applied to the Diseases and Accidents incident to Women. By W. H. BYFORD, A.M., M.D., Professor of Gynæcology in Rush Medical College, and of Obstetrics in the Woman's Medical College, and HENRY T. BYFORD, M.D., Surgeon to the Woman's Hospital, Chicago. Fourth Edition. With 306 Engravings. Royal 8vo, 25s.

DUNCAN.—**Clinical Lectures on the Diseases** of Women. By J. MATTHEWS DUNCAN, M.D., F.R.C.P., F.R.S., Obstetric Physician to St. Bartholomew's Hospital. Third Edition. 8vo, 16s.

WOMEN, DISEASES OF—*continued.*

GALABIN.—**The Student's Guide to the Diseases of Women.** By ALFRED L. GALABIN, M.D., F.R.C.P., Obstetric Physician to Guy's Hospital, Examiner in Obstetric Medicine to the University of Cambridge, and to the R. C. P. Lond. Fourth Edition. With 94 Engravings. Fcap. 8vo, 7s. 6d.

REYNOLDS.—**Notes on Diseases of Women.** Specially designed to assist the Student in preparing for Examination. By J. J. REYNOLDS, L.R.C.P., M.R.C.S. Third Edition. Fcap. 8vo, 2s. 6d.

SAVAGE.—**The Surgery of the Female Pelvic Organs.** By HENRY SAVAGE, M.D., Lond., F.R.C.S., one of the Consulting Medical Officers of the Samaritan Hospital for Women. Fifth Edition, with 17 Lithographic Plates (15 Coloured), and 52 Woodcuts. Royal 4to, 35s.

WEST AND DUNCAN.—**Lectures on the Diseases of Women.** By CHARLES WEST, M.D., F.R.C.P. Fourth Edition. Revised and in part re-written by the Author, with numerous additions by J. MATTHEWS DUNCAN, M.D., F.R.C.P., F.R.S., Obstetric Physician to St. Bartholomew's Hospital. 8vo, 16s.

ZOOLOGY.

CHAUVEAU AND FLEMING.—**The Comparative Anatomy of the Domesticated Animals.** By A. CHAUVEAU, Professor at the Lyons Veterinary School; and GEORGE FLEMING, Principal Veterinary Surgeon of the Army. With 450 Engravings. 31s. 6d.

HUXLEY.—**Manual of the Anatomy of Invertebrated Animals.** By THOMAS H. HUXLEY, LL.D., F.R.S. With 156 Engravings. Post 8vo, 16s.

By the same Author.

Manual of the Anatomy of Vertebrated Animals. With 110 Engravings. Post 8vo, 12s.

WILSON.—**The Student's Guide to Zoology: a Manual of the Principles of Zoological Science.** By ANDREW WILSON, Lecturer on Natural History, Edinburgh. With Engravings. Fcap. 8vo, 6s. 6d.

Riley Dunn & Wilson Ltd
EXPERT CONSERVATORS & BOOKBINDERS