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# HAND-BOOK

OF

# PHYSIOLOGY.

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# HAND-BOOK

OF

# PHYSIOLOGY.

BY

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# PREFACE TO THE FOURTH EDITION.

In the preparation of the present Edition, every portion of the work has been submitted to careful revision; several of the subjects have been re-written, and in nearly all parts various alterations and additions have been introduced. By devoting as much time as other engagements would allow me, I have endeavoured to bring the work, as nearly as possible, to a level with the present knowledge of the Science of Physiology.

A slight increase in the size of the book having been adopted, a corresponding diminution in the number of the pages has resulted, while the amount of matter remains fully as great as before.

No change, however, has been made in the general plan and arrangement of the book; and no more detailed account of the structure of organs and tissues is given, because of the increased bulk which such an addition would have occasioned, and because of the number and excellence of the published works on General and Physiological Anatomy. This explanation seems to be the more necessary, because of my desire to comply with the suggestions of several friendly advisers that I should introduce a fuller description of

the various structures of the body; for the reasons stated, however, I have thought it best to adhere to the original plan. The work therefore remains as it was before, essentially a Hand-book of Physiology.

I desire to express my grateful acknowledgments, for many services rendered in the preparation of this Edition, to my friend and colleague Mr. Savory, Professor of Comparative Anatomy and Physiology to the Royal College of Surgeons.

WILLIAM SENHOUSE KIRKES.

Lower Seymour-street,
September 29th, 1860.

# PREFACE TO THE FIRST EDITION.

THE publishers of Dr. Baly's edition of "Müller's Elements of Physiology" had long designed to render that admirable work more available for the general use of students. They had proposed the reduction of its principal contents into a volume more nearly proportionate to the share of time which can be devoted to Physiology, as only one of many subjects to be studied in the period of pupillage. The present work was commenced with the intention of fulfilling their design; it was announced as a "Hand-book of Physiology on the Basis of Müller's Elements;" and many of its chapters, namely, those on MOTION, VOICE and SPEECH, THE SENSES, GENERATION, and DEVELOPMENT, are chiefly abstracts of corresponding portions of that work, and of the Supplement by Dr. Baly and myself. But, in the rest of the subjects, it was found that the progress of Physiology, during seven years, had so increased or modified the facts, and some even of the principles of the science, that "Müller's Elements," and the notes added by Dr. Baly, could only be employed as among the best authorities and examples. The design was, therefore, departed from, so far as it concerned the construction of a Hand-book on the basis of Müller.

In writing the present work, the primary object has been to give such an account of the facts and generally admitted principles of Physiology as may be conveniently

consulted by any engaged in the study of the Science; and, more especially, such an one as the student may most advantageously use during his attendance upon lectures, and in preparing for examinations. The work essential to this plan required that only so much of Anatomy, Chemistry, and the other sciences allied to Physiology, should be introduced as might serve to remind the reader of knowledge already acquired, or to be obtained, by the study of works devoted to these subjects. For the same end, it was necessary to omit all discussions of unsettled questions, and expressions of personal opinion; but ample references are given, not only to works in which these may be read, but to those by which the study of Physiology may be, in its widest extent, pursued.

For the convenience of students the subjects are arranged on a plan corresponding with that in which they are taught in the courses of Lectures on Physiology, delivered in the principal metropolitan schools of medicine.

I cannot sufficiently express my obligations to Mr. Paget, from whom I have received the most liberal aid, in every stage of the work; and who has, moreover, afforded me access to his manuscript notes of Lectures. I have also to offer my best thanks to Dr. Baly for many kind suggestions made by him in the course of the work.

WILLIAM SENHOUSE KIRKES.

Sept. 29th, 1848.

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# EXPLANATION OF PLATES.

Figs. 1 to 5 represent the particles from the blood of different animals, all magnified about four hundred diameters.

Fig. 1. Red particles of human blood, after Wagner.

Fig. 2. Red particles of the blood of the common fowl. *a*, Ordinary appearance when the flat surface is turned towards the eye; *b*, appearance which is sometimes presented by the particle when in the same position, and which suggests the idea of a furrow surrounding the central nucleus; *c*, *d*, different appearances of the particles when seen edgeways.

Fig. 3. Red particles of the frog.

Fig. 4. ———— of the Squalus squatina, after Wagner.

Fig. 5. ———— of the Lophius piscatorius, after Wagner.

## PLATE II.

Fig. 3. Fibres of elastic tissue from the ligamentum flavum of the vertebræ (magnified about three hundred and eighty diameters).

Fig. 4. Fasciculi and fibres of cellular tissue (magnified about six hundred diameters).

Fig. 5. Portion of tendon (magnified about six hundred diameters).

Fig. 6. Portion of the middle fibrous coat of the aorta (magnified about three hundred and eighty diameters).

Fig. 7. Muscular fibres of animal life (magnified about two hundred diameters).

Fig. 8. Portion of a broken muscular fibre of animal life (magnified about seven hundred diameters).

Fig. 9. Organic muscular fibres (magnified three hundred and fifty diameters).

## PLATE III.

This is the drawing of an embryo, with its membranes, in the possession of Dr. Sharpey, of which an outline copy and a full description are given at page 657.

## PLATE IV.

Figs. 1, 2, 3, are drawings of an ovum and embryo, representing different views of the umbilical vesicles; after Müller.

Fig. 5 represents the second embryo belonging to Dr. Sharpey, described at page 674.

Fig. 4 represents the mesentery and intestine of the embryo shewn in Plate III., spread out so as to display the mesenteric vessels, and the origin of the omphalo-mesenteric artery from one of the main branches. See the description at pages 657-8.

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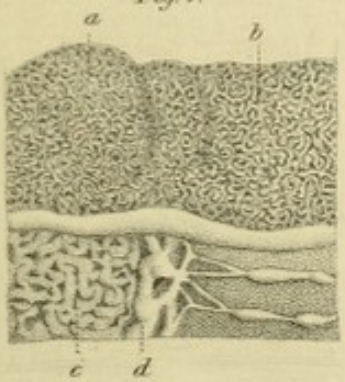
These plates, as well as most of the wood-engravings, are adopted from Dr. Baly's edition of Müller's Physiology.

Fig. 7.

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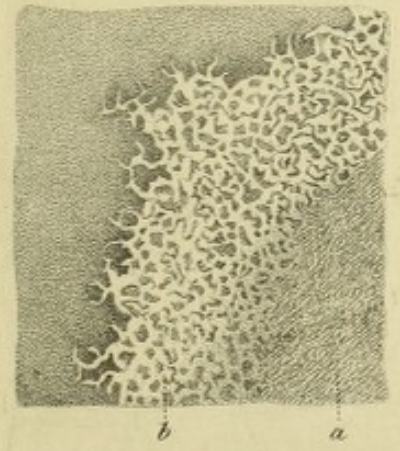
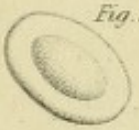



Fig. 9.

Fig. 1.

Fig. 2.

Fig. 3.



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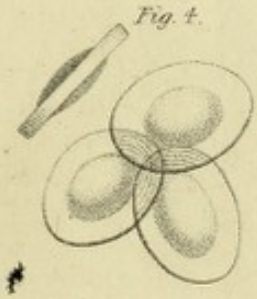

Fig. 5.

H. Adlard sc.

Fig 3.

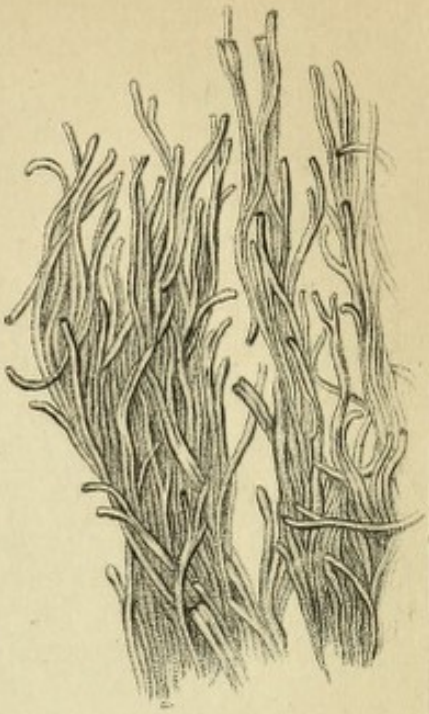

Fig. 5.

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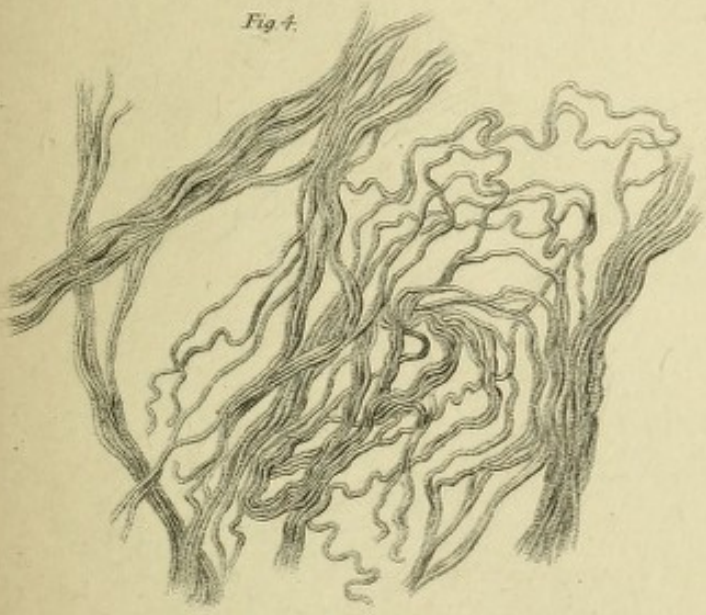

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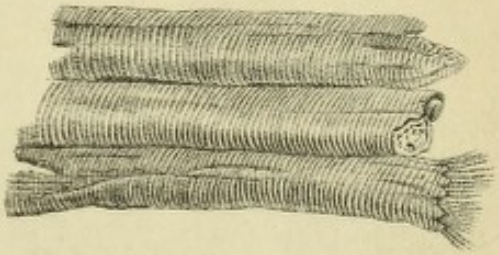

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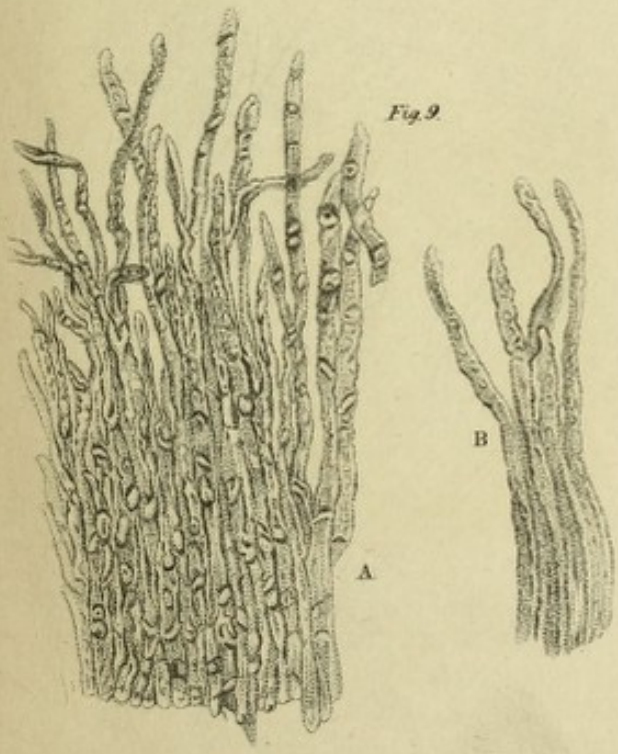


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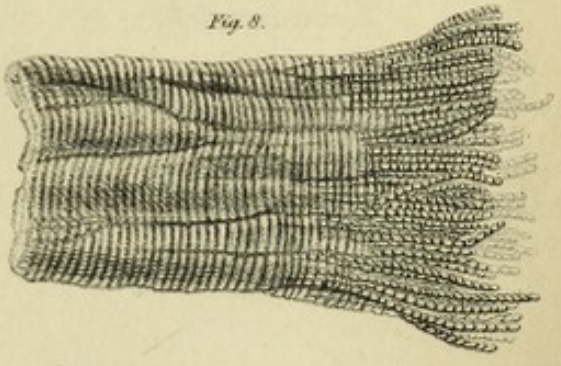

DRAWN BY J. HASLOCH – ENGRAVED BY CHARLES WASS.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 1.

Charles Wass, sc.

# HANDBOOK OF PHYSIOLOGY.

## INTRODUCTION.

HUMAN PHYSIOLOGY is the science which treats of the conditions, phenomena, and laws of the life of the human body in the state of health.

The phenomena of life manifested in the human body, as in that of all animals, may be arranged in two principal classes; the first comprehending those which are observed, in various degrees of perfection and variously modified, in both vegetables and animals; the second, those which are peculiar to the members of the animal kingdom.

The first class of the phenomena of life includes, 1st. The processes of digestion, absorption, secretion, excretion, circulation, and respiration, which, together with the offices of some parts not yet understood, fulfil their purpose in the formation, movement, and purification of the blood, with the materials for the nutrition of all the tissues of the body; 2nd. The processes of growth and nutrition, or nutritive assimilation, by which the several parts of the body, obtaining materials from the blood, repair the loss and waste to which they are subject in the discharge of their functions, or through their natural impairment and decay; 3rd. The generative processes, for the formation, impregnation, and development of the ova.

These are named processes, functions, or phenomena of *organic* or *vegetative* life. Those of the first two divisions maintain the existence of the individual being; those of the third maintain that of the species.

The second class of vital phenomena includes the functions of sensation and voluntary motion, by which the mind of an animal acquires knowledge of things external to itself, and is enabled to act upon them. These are named phenomena of *animal* or *relative* life.

But the division of the functions or phenomena of life into these, or any similar classes, is artificial, and must not be taken as indicating absolute difference and dissociation. The organic and the animal life are knit together and mutually dependent; neither can be long maintained without the other. As all the processes of organic life are essential to the maintenance of the organs of animal life, so, in an equal degree, the sensation and voluntary motion of animal life are essential to the taking of food, the discharge of excretions, and other processes of organic life, by which the animal and the species are maintained.

All the bodies in which the phenomena of life have been observed are formed of diverse mutually adapted parts, or organs; they are, therefore, called organisms, or organised bodies or parts; their composition and structure, being peculiar, are named organic, and constitute their organisation. While alive, also, they manifest certain peculiar *vital* properties and modes of action. A brief account, therefore, of the chemical composition, general anatomical structure, and vital properties of the several tissues and organs, will be a necessary preface to the consideration of their actions.

# CHAPTER I.

## CHEMICAL COMPOSITION OF THE HUMAN BODY.

The following *Elementary Substances* may be obtained by chemical analysis, from the human body; Oxygen, Hydrogen, Nitrogen, Carbon, Sulphur, Phosphorus, Silicon, Chlorine, Fluorine, Potassium, Sodium, Calcium, Magnesium, Iron, and probably, or sometimes, Manganesium, Aluminium, and Copper.

Thus, of the sixty-five elements of which all known matter is composed, nearly one-third exist in the human body. A few others have been detected in the bodies of other animals; but no element has yet been found in any living body which does not also exist in inorganic matter.

Of the elements enumerated above, the first four, because they exist in nearly all animal substances and form the largest parts of all, are named *essential elements;* the rest, being less constant, and occurring often in only very small quantity, are named *incidental elements*. But the term *incidental* must not be understood to imply that any of these elements (except, perhaps, the last three) are less necessary to the right composition of the substances in which they exist than the essential elements are. Sulphur, for example, is as constant and necessary a constituent of albumen, and iron of hæmatosine, as any of the elements are. The terms must be taken in only a general sense. No organic substance being known which has not at least two, and the great majority having three or all of the first four elements, they may be considered essential to the formation and existence of organic matter. But one or more of the other elements added to these, in comparatively small proportions, contribute to determine, as it were incidentally, the peculiarities by which one kind of organic matter is distinguished from another.

The elements composing organic and inorganic matter being thus the same, we must look to the modes in which they are

combined for an explanation of the differences between the two classes of substances. We cannot indeed draw an absolute rule of chemical distinction between the two classes, for there are substances which present every gradation of composition between those that are quite organic and those that are inorganic. Such substances of intermediate composition are those that are formed when inorganic matters, taken as nutriment by plants, gradually assume the characters of organic matter, under the influence of the vital properties of the plant; and such are those which are formed in both plants and animals, when, out of the well-organised tissues, or out of the sap or blood, materials are being separated, to form either tissues for mechanical service, or stores for nutriment, or purifying excretions. In both cases, the substances that are in the state of transition between the organic and the inorganic, or between the more and the less organised states, may proceed through changes so gradual that no natural line of demarcation between the two states can be discerned; and one cannot say when that which has been called inorganic has acquired the characters of an organic body, or when that which has been organic ceases to deserve the name. Alcohol, ether, acetic acid, urea, uric acid, and the fatty and oily matters, are such substances of organic origin, and intimately related to such as no one would hesitate to call organic, yet in their simplicity and mode of composition they are like inorganic matters.

But although no decided difference in chemical characters can be discerned in substances that thus stand, as it were, on the boundary between the organic and the inorganic world, yet, all the substances that form the proper component living tissues of animal bodies are as distinguished from inorganic substances as the actions of living bodies are from the passiveness of dead; and, as a general rule, it may be held that the more active the vital processes are that are carried on in any substance, the more widely do the chemical characters of that substance differ from those of inorganic matter.

Among the *peculiarities in the chemical characters* of animal substances the two following may be specially noticed:—

1. The simplest of the compounds naturally formed in the body,—of those compounds which, from their being supposed to stand, in order of simplicity, nearest to the elements, are called *proximate principles*,—are composed of at least three elements. In the inorganic world, the most abundant substances are either in the elemental state, as the oxygen and nitrogen, by the mixture of which the atmosphere is formed; or, are formed by the union of only two elements, as water, of oxygen and hydrogen, the oxides of calcium, aluminium, and others. In the organic world, the most abundant substances are, in plants, compounds of three elements, as starch, gum, sugar, cellulose, and others composed of carbon, hydrogen, and oxygen; and in animals, of four or five elements, as albumen, fibrine, gelatine, and other compounds of the four essential elements, and sulphur.

2. Not only are a large number of elements usually combined in an organic compound, but a large number of equivalents or atoms of each of the elements are united to form an equivalent or atom of the compound. In the case of carbonate of ammonia, as an example among inorganic substances, one equivalent of carbonic acid is united with one of ammonia; the equivalent or atom of carbonic acid consists of one of carbon with two of oxygen; and that of ammonia of one of nitrogen with three of hydrogen. But in an equivalent or atom of fibrine, or of albumen, there are of the same elements, respectively, 48, 15, 12, and 39 equivalents, according to Dumas, and nearly ten times as many according to Mulder. And, together with this union of large numbers of equivalents in the organic compound, it is further observable, that the several numbers stand in no simple arithmetical relation one with another, as the numbers of equivalents combining in an organic compound do.

With these peculiarities in the chemical composition of organic bodies we may connect two other consequent facts: the first, that of the large number of different compounds that are formed out of comparatively few elements; the second, that of

their great proneness to decomposition. For it is a general rule, that the greater the number of equivalents or atoms of an element that enter into the formation of an atom of a compound, the less is the stability of that compound. Thus, for example, among the various oxydes of lead and other metals, the least stable in their composition are those in which each equivalent has the largest number of equivalents of oxygen. So, water, composed of one equivalent of oxygen and one of hydrogen, is not changed by any slight force; but peroxyde of hydrogen, which has two equivalents of oxygen to one of hydrogen, is among the substances most easily decomposed.

The instability, on this ground, belonging to animal organic compounds is augmented, 1st, by their containing nitrogen, which, among all the elements, may be called the least decided in its affinities, that which maintains with least tenacity its combinations with other elements; and, 2ndly, by the quantity of water which, in their natural mode of existence, is combined with them, and the presence of which furnishes a most favourable condition for the decomposition of nitrogenous compounds. Such, indeed, is the instability of animal compounds, arising from these several peculiarities in their constitution, that, in dead and moist animal matter, no more is requisite for the occurrence of decomposition than the presence of atmospheric air and a moderate temperature; conditions so commonly present that the decomposition of dead animal bodies appears to be, and is generally called, spontaneous. The modes of such decomposition vary according to the nature of the original compound, the temperature, the access of oxygen, the presence of microscopic organisms, and other circumstances, and constitute the several processes of decay and putrefaction; in the results of which processes the only general rule seems to be, that the several elements of the original compound finally unite to form those substances whose composition is, under the circumstances, most stable.*

* An interesting account of the nature of the so-called spontaneous decomposition of dead organic matter is given by Dr. Helmholtz (lxxx. 1843): for an abstract of the paper see xxv. 1843-4, p. 5. The

It is not known how far the process of decomposition which thus occurs in dead animal matter is imitated in the living body; but the facility of decomposition which it indicates may be considered in the study of those chemical changes which are constantly effected during life tranquilly, and without the intervention of any such comparatively violent forces as are used in chemical art. The instability which organic compounds shew, when dead, makes them amenable to the chemical forces exercised on them during life by the living tissues—forces inimitably gentle, so slight that their operation is not discernible by any effects besides those which they produce in the living body.

What has been said respecting the mode in which the elements are combined in the composition of animal matter refers only to the four essential elements. Little or nothing is known of the mode in which the incidental elements, or their compounds, are combined with the compounds formed of the essential elements; only it is probable that they are combined chemically, and as necessary parts of the substances they contribute to form.

Of the *natural organic compounds* existing in the human body, some occur almost exclusively in particular tissues or fluids; as the colouring matter of the blood and other fluids, the fatty matter of the nervous organs, etc. But many exist in several different parts, and may, therefore, be now described in general terms.

They may be arranged in two classes, namely, the azotized, or nitrogenous, and the non-azotized or non-nitrogenous principles.

The *non-azotized principles* include the several fatty, oily, or

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experiments of Helmholtz show, that although the results of spontaneous decomposition are modified by the presence of infusorial organisms, yet these are not, as has been supposed, essential to the occurrence of the process: their existence in large quantities in decomposing animal matters is due to the fact, that such decomposition furnishes the most favourable conditions to their development and life. Consult, also, on this subject, Liebig, in the last edition of his Animal Chemistry.

oleaginous substances, of which, in the human body, the most abundant are named margarine, elaine or oleine, stearine, cholestearine, and cerebrine.

The *fatty substances* are, nearly all, compounds of carbon, hydrogen, and oxygen. They burn with a bright flame, the proportion of oxygen being less than would be sufficient to form water with the hydrogen, or carbonic acid with the carbon, that they contain. They are all lighter than water, nearly all are fluid at the natural temperature of the body, all are insoluble in water, soluble in ether and boiling alcohol, and most of them crystallize when deposited from solution. They are nearly all of the kind named *fixed oils;* none of them is what is called a *drying oil*, *i. e.*, none so combines with oxygen as to form a resin-like varnish on the substance over which it is spread.

The oily or fatty matter which, enclosed in minute cells, forms the essential part of the adipose or fatty tissue of the human body, and which is mingled in minute particles in many other tissues and fluids, consists of a mixture of margarine and oleine, the proportion of the former being the greater the higher the temperature at which the mixture congeals, and the firmer the mass is when congealed. The animal fats, or *suets*, that are firmer than human fat, contain also a substance named stearine, which remains solid at or near 130° F. Margarine congeals at about 120°, oleine at about 25°. Their mixture in human fat is a clear yellow oil, of which different specimens congeal at from 45° to 35° F. Margarine when deposited from solution in alcohol, forms fine needle-shaped crystals; and microscopic tufts or balls of such crystals are often found in fat-cells after death, especially in the fat of diseased parts and old people.

Margarine and oleine, like all the fatty matters with which soaps may be made, and which are therefore named *saponifiable*, appear to consist of fatty acids combined with a base which is soluble in water. When one of these fats is long boiled with an alkali, it is decomposed: the fatty acid, which is named

margaric or oleic, according to the substance employed, unites with the alkali, forming a neutral soapy substance, margarate or oleate of soda, or potash, as the case may be: and the base of the fat, a sweet syrupy substance named *glycerine*, remains. The fatty matter of human adipose tissue may therefore be regarded as a mixture of margarate and oleate of glycerine. Glycerine, moreover, is considered to be a hydrated oxyde of a substance called Glyceryl; and margaric acid a compound of a substance named Margaryl with oxygen.

*Cholestearine* or *Cholesterine*, a fatty matter which does not melt below 278°, and is, therefore, always solid at the natural temperature of the body, may be obtained in small quantity from blood, bile, and nervous matter. It occurs abundantly in many biliary calculi; the pure white crystalline specimens of these concretions being formed of it almost exclusively. Minute rhomboidal scale-like crystals of it are also often found in morbid secretions, as in cysts, the puriform matter of softening and ulcerating tumours, etc. It is soluble in ether and boiling alcohol; but alkalies do not change it; it is one of those fatty substances which are not saponifiable.

The *azotized* or *nitrogenous principles* in the human body include two chief classes of substances, namely the gelatinous and the albuminous.

The *gelatinous substances* are contained in several of the tissues, especially those which serve a passive mechanical office in the economy; as the cellular or fibro-cellular tissue in all parts of the body, the tendons, ligaments, and other fibrous tissues, the cartilages and bones, the skin and serous membranes. These when boiled in water, yield a material, the solution of which remains liquid while it is hot, but becomes solid and jelly-like on cooling.

Two varieties of these substances are described, *gelatine* and *chondrine*, the latter being derived from cartilages, the former from all the other tissues enumerated above, and in its purest state, from isinglass, which is the swimming-bladder of the sturgeon, and which, with the exception of about 7 per cent.

of its weight, is wholly reducible into gelatine. The most characteristic property of gelatine is that already mentioned, of its solution being liquid when warm, and solidifying or setting when it cools. The temperature at which it becomes solid, the proportion of gelatine which must be in solution, and the firmness of the jelly when formed, are various, according to the source, the quantity, and the quality of the gelatine; but, as a general rule, one part of dry gelatine dissolved in 100 of water, will become solid when cooled to 60°. The solidified jelly may be again made liquid by heating it; and the transitions from the solid to the liquid state by the alternate abstraction and addition of heat, may be repeated several times; but at length the gelatine is so far altered, and, apparently, oxydised by the process, that it no longer becomes solid on cooling. Gelatine in solutions too weak to solidify when cold, is distinguished by being precipitable with alcohol, creasote, tannic acid, and bichloride of mercury, and not precipitable with the ferrocyanide of potassium. The most delicate and striking of these tests is the tannic acid, which is conveniently supplied in an infusion of oak-bark or gall-nuts: it will detect one part of gelatine in 5000 of water; and if the solution of gelatine be strong it forms a singularly dense and heavy precipitate, which has been named tanno-gelatine, and is completely insoluble in water.

When gelatine is boiled with caustic potash, or with sulphuric acid, it is decomposed, and among the products of its change are two substances named leucine and sugar of gelatine, of which the latter is remarkable for its similarity to the sugars produced from vegetable substances, and for being susceptible of crystallization (Simon, lxxxii. vol. i. p. 195, and Prout, xxi. p. 455; see also lix. 1850, p. 96, and 1855, p. 116).

Among the varieties of gelatine derived from different tissues, and from the same sources at different ages, much diversity exists as to the firmness and other characters of the solid formed in the cooling of the solutions. The differences between isinglass, size, and glue, in these respects, are familiarly known, and

afford good examples of the varieties called weak and strong, or low and high, gelatines. The differences are ascribed by Dr. Prout to the quantities of water combined in each case with the pure or anhydrous gelatine; and part of this water seems to be chemically combined with the gelatine, for no artificial addition of water to glue would give it the character of size, nor would any abstraction of water from isinglass or size convert it into the hard dry substance of glue. But such a change is effected in the gradual process of nutrition of the tissues; for, as a general rule, the tissues of an old animal yield a much firmer or stronger jelly than the corresponding parts of a young animal of the same species. A similar difference is observable in the leathers formed by the tanning of the skins of young and old animals; a fact which, together with the general similarity of the action of tannic acid upon skin and upon gelatine, makes it probable that gelatine is really (though some chemists hold the contrary), contained as such in the tissues from which it is obtained by boiling.

*Chondrine.*—The variety of gelatine obtained from cartilages agrees with gelatine in that its solution in water solidifies on cooling, though less firmly, and is precipitable with alcohol, creasote, tannic acid, and bichloride of mercury. Like gelatine, also, it is distinguished from the albuminous substances by not being precipitable with ferrocyanide of potassium; and, by assuming a yellowish-brown, instead of a red colour, when tested by sulphuric acid and sugar (Schultze, lix. 1850, p. 102); but, unlike gelatine, it is precipitable with acetic and the mineral and other acids, and with the sulphate of alumina and potash, persulphate of iron and acetate of lead.

The *albuminous substances* are more highly or perfectly organic, *i.e.*, are more different from inorganic bodies than are any of the substances yet considered, or, perhaps, any in the body. The chief among them are, albumen, fibrine, and caseine; the last is found almost exclusively in milk. Principles essentially similar to them all are found also in vegetables, especially in the sap and fruits. And substances much resembling,

though not classed with, the albuminous, are horny matter and extractive matter.

*Albumen* exists in some of the tissues of the body, especially the nervous, in the lymph, chyle, and blood, and in many morbid fluids, as the serous secretions of dropsy, pus, and others. In the human body it is most abundant, and most nearly pure, in the serum of the blood. In all the forms in which it naturally occurs, it is combined with about six per cent. of fatty matter, phosphate of lime, chloride of sodium, and other saline substances. Its most characteristic property is, that both in solution, and in the half-solid state in which it exists in white-of-egg, it is coagulated by heat, and in thus becoming solid, becomes insoluble in water. The temperature required for the coagulation of albumen is the higher the less the proportion of albumen in the solution submitted to heat. Serum and such strong solutions will begin to coagulate at from 150° to 170°, and these, when the heat is maintained, become almost wholly solid and opaque. But weak solutions require a much higher temperature, even that of boiling, for their coagulation, and either only become milky or opaline, or produce flocculi which are precipitated.

Albumen, in the state in which it naturally occurs, appears to be but little soluble in pure water, but is soluble in water containing a small proportion of alkali. In such solutions it is probably combined chemically with the alkali; it is precipitated from them by alcohol, ether, nitric, and other mineral acids (unless when they are very dilute), by ferrocyanide of potassium (if before or after adding it the alkali combined with the albumen be neutralised), by bichloride of mercury, acetate of lead, and most metallic salts. These precipitates are not merely solidified albumen, but compounds of albumen, with the acid or base added to it. In the former case, the albumen takes the part of a base, as in nitrate of albumen; in the latter, it takes the part of an acid, as in albuminate of oxyde of mercury, lead, etc. The precipitates with the metallic salts are soluble in an excess of albumen, and in

solutions of chloride of sodium and other alkaline salts; and it is, probably, by these means that the salts of iron, mercury, and other metals, taken into the blood, remain dissolved in it.

Coagulated albumen, *i.e.*, albumen made solid with heat, is soluble in solutions of caustic alkali, and in acetic acid if it be long digested or boiled with it. With the aid of heat, also, strong hydrochloric acid dissolves albumen previously coagulated, and the solution has a beautiful purple or blue colour.

The per-centage composition of albumen of blood, according to the experiments of Mulder (lix. 1847, p. 83), is, carbon, 53·4; hydrogen, 7·1; nitrogen, 15·6; oxygen, 22·3; phosphorus, 0·3; sulphur, 1·3: its formula is not yet certainly known.

*Fibrine* exists, most abundantly, in solution in the blood and the more perfect portions of the lymph and chyle. Its characteristic property is, that in certain conditions (especially when the blood or other fluid containing it is taken from the living body), it separates from its solution, and spontaneously assumes the solid form, or coagulates.* It is on this that the coagulation of the blood (a process to be further described hereafter) depends. If a common clot of blood be pressed in fine linen while a stream of water flows upon it, the whole of the blood-colour is gradually removed, and strings and various pieces remain of a soft, yet tough, elastic, and opaque-white substance, which consist of fibrine, impure with a mixture of fatty matter, lymph-corpuscles, shreds of the membranes of red blood-corpuscles, and some saline substances. Fibrine somewhat purer than this may be obtained by stirring blood while it coagulates, and collecting the shreds that attach themselves to the instrument, or by retarding the coagulation, and, while the red

* A very small quantity of fibrine may be so dissolved in serous fluid that it will not spontaneously coagulate. The fluid of common hydrocele does not of itself coagulate; but, as Dr. Buchanan (lxxi. 1836, pp. 52, and 90; 1845, p. 617) has shown, if a piece of washed clot of blood, or of muscle, or some other animal tissue be placed in it, a filmy coagulum of fibrine will form and attach itself to the substance introduced. The film has the filamentous appearance of proper fibrine clot, and is not mixed with corpuscles, as that of blood-clot is.

blood-corpuscles sink, collecting the fibrine unmixed with them. But in neither of these cases is the fibrine perfectly pure.

Chemically, fibrine and albumen can scarcely be distinguished. All the changes, produced by various agents, in coagulated albumen may be repeated with coagulated fibrine, with no greater differences of result than may be reasonably ascribed to the differences in the mechanical properties of the two substances. Of such differences, the principal are, that fibrine immersed in acetic acid swells up and becomes transparent like gelatine, while albumen undergoes no such apparent change; and that deutoxyde of hydrogen is decomposed when in contact with coagulated fibrine, but not with albumen.

Mulder originated the opinion that animal albumen, fibrine, and caseine, and the corresponding substances derived from vegetables, are all compounds of a substance which he named *proteine*, and believed to be composed of the four essential elements alone. Liebig and others, however, deny the existence of any such substance as *proteine*. Whichever be the correct view, we may be justified in still retaining the use of the term *proteine-compounds*, in speaking of the class, including fibrine, albumen, and others to which the name of *albuminous compounds* was originally applied: the two terms may be used synonymously.*

*Horny Matter.*—The substance of the horny tissues, including the hair and nails (with whale-bone, hoofs, and horns), consists of a *proteine-compound*, with larger proportions of sulphur than albumen and fibrine contain. Hair contains 10 per cent. and nails 6·8 per cent. of sulphur.

The horny substances, to which Simon applied the name of keratine, are insoluble in water, alcohol, or ether; soluble in caustic alkalies, and sulphuric, nitric, and hydrochloric acids; and not precipitable from the solution in acids by ferrocyanide of potassium.

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* For a full account of proteine-compounds generally, see Lehmann's Physiological Chemistry (Cavendish Society's Edition), vol. i. pp. 326—404.

*Mucus*, in some of its forms, is related to these horny substances, consisting, in great part, of epithelium detached from the surface of mucous membrane, and floating in a peculiar clear and viscid fluid. But, under the name of mucus, several various substances are included, of which some are morbid albuminous secretions containing mucus and pus-corpuscles, and others consist of the fluid secretion variously altered, concentrated, or diluted. But the true chemical characters of this fluid are as yet incompletely known. It is generally alkaline, and, when the cells and other corpuscles mingled with it have subsided, is a pellucid fluid, containing, according to Berzelius, 5·33 per cent. of proper mucous matter. This is very little soluble in water; more soluble in water slightly alkaline, and from this solution is precipitated by alcohol, acetic, nitric, sulphuric, and hydrochloric acids. An excess of the last three acids redissolves the precipitates they severally throw down; and, in the acid solution thus formed, ferrocyanide of potassium produces no precipitate. According to Scherer (x. b. 57), pure mucus, cleared of epithelium, and subtracting 4·1 per cent. of saline matter, contains carbon 52·17, hydrogen 7·01, nitrogen 12·64, oxygen 28·18.

*Extractive Matters.*—Under this name are included substances of mixed and uncertain composition, which form the residue of animal matter when, from almost any of the fluids or solids of the body, the albuminous, gelatinous, and fatty principles have been removed. The remaining animal matter is mixed with various salts, such as lactates, chlorides, and phosphates, and is divisible into two principal portions, of which one is soluble in water alone, the other in alcohol.

Doubtless there are in these substances many distinct compounds, of which some exist ready-formed in the body, and some are formed in the changes to which the previous chemical examinations have given rise. Many of them, including kreatine and kreatinine, two principles originally discovered among the extractive matters of muscular tissue, but since found in the blood, urine, and elsewhere, are no doubt pro-

ducts of the chemical changes that take place in the natural waste and degeneration of the tissues, and are substances that are to be separated from the tissues for excretion.

Such are the chief substances of which the human body is composed. They are formed mainly of the four essential elements, and exhibit all those characters which have been mentioned as peculiar to organic bodies ; but, with the exception of the fatty matters, all appear to contain, besides the four elements, other elements, or even compound substances, such as phosphate of lime, chloride of sodium, or other salts. And all the fluids and tissues of the body appear to consist, chemically speaking, of mixtures of several of these principles, together with saline matters. Thus, for example, a piece of muscular flesh would yield fibrine, albumen, gelatine, fatty matters, salts of soda, potash, lime, magnesia, iron, and other substances which appear passing from the organic towards the inorganic states, as kreatine and others. This mixture of substances may be explained in some measure by the existence of many different structures or tissues in the muscles; the gelatine may be referred principally to the cellular tissue between the fibres, the fatty matter to the adipose tissue in the same position, and part of the albumen to the blood and the fluid by which the tissue is kept moist. But, beyond these general statements, little can be said of the mode in which the chemical compounds are united to form an organised structure; or of how, in any organic body, the several inorganic and incidental substances are combined with those that are organic and essential. It must suffice, therefore, to mention the several parts in which each of the incidental elements and of their principal compounds occurs.

*Sulphur* is probably, next to the essential ones, the most nearly constant element in organic compounds. It exists in albumen, fibrine, caseine, and gelatine, combined in all these, probably in the elemental state, with the other elements. In largest proportion, it is found in taurine, one of the products of the decomposition of biliary matter, and in the morbid pro-

duct, cystic oxide: of both these it constitutes about 25 per cent. Among the tissues, and independent of the compounds above-named as containing it, sulphur is most abundant in the hair, cuticle, nails, and other horny tissues, and according to Lassaigne (lv. Aug. 22, 1843), in fibrous and mucous membranes. Of the compounds of sulphur none are known to exist naturally, except the sulphocyanide of potassium in saliva, and the sulphates in the urine and sweat. The acid of the sulphates found in the ashes of other animal substances are formed during the burning, through the elemental sulphur combining with oxygen.

*Phosphorus* is found together with sulphur, and probably similarly combined as an element, in albumen and fibrine, but not in caseine. It exists also in some tissues, especially in the substance of the brain, from which two fatty acids, containing phosphorus, and named oleo-phosphoric and cerebric acid, have been obtained; but, most abundantly, it occurs as phosphoric acid in combination with alkaline and earthy bases—as in the tribasic phosphate of soda in the blood and saliva, the superphosphates of the muscles and urine, the basic phosphate of lime and magnesia in the bones and teeth. Such phosphates are also found in the ashes of nearly all burnt animal substances, even in tissues so simple that one must assume the phosphate to be a necessary constituent of the substance of the primary cell; for it is probable that these phosphates exist in the tissues ready formed, as they do in caseine, and that they are not, like the sulphates found in the ashes of animal matters, produced in the combustion.

*Silicon.*—A very small quantity of silica exists, according to Berzelius, in the urine, and, according to Henneberg (x. Bd. 41) and E. Millon (xviii. 1848), in the blood. Traces of it have also been found in bones by V. Bibra, in hair by Van Laer, and in some other parts of the body (lxv. p. 65).

*Chlorine* is abundant in combination with sodium, potassium, ammonium, and other bases in all parts, fluid as well as solid, of the body. Chloride of sodium (common salt) is,

indeed, probably the most universal of all the inorganic compounds in organised bodies. In the form of hydrochloric acid, either free or in combination with an organic principle, it is also sometimes found in the gastric fluid.

*Fluorine.*—The observations of Berzelius, on which the existence of minute quantities of fluoride of calcium in the bones, teeth and urine, was admitted, after having been much questioned, have been fully confirmed by Dr. Daubeny and Mr. Middleton (lxiii. vol. ii. pp. 97, 134), and more recently by Von Bibra (lxiv.) The salt is found in the ashes of all bones and teeth; and increased in quantity in fossil bones.

*Potassium* and *sodium* are constituents of the blood and all the fluids, in various quantities and proportions. They exist in the form of chlorides, sulphates, and phosphates, and probably, also, in combination with albumen, or certain organic acids. Liebig, in his work on the Chemistry of Food, has shewn that the juice expressed from muscular flesh always contains a much larger proportion of potash-salts than of soda-salts; while in the blood and other fluids, except the milk, the latter salts always preponderate over the former; so that, for example, for every 100 parts of soda-salts in the blood of the chicken, ox, and horse, there are only 40·8, 5·9, and 9·5 parts of potash-salts; but for every 100 parts of soda-salts in their muscles there are 381, 279, and 285 parts of potash-salts.

*Calcium.*—The salts of lime (oxide of calcium) are by far the most abundant of the earthy salts found in the human body. They exist in the lymph, chyle, and blood in combination with phosphoric acid, the phosphate of lime being probably held in solution by the presence of phosphate of soda. Perhaps no tissue is wholly void of phosphate of lime; but its especial seats are the bones and teeth, in which, together with carbonate of lime and fluoride of calcium, it is deposited in minute granules, in a peculiar compound, named bone-earth, and containing 51·55 parts of lime, and 48·45 of phosphoric acid. Phosphate of lime, probably the tribasic

phosphate, is also found in the saliva, milk, bile, and most other secretions, and superphosphate in the urine, and probably in the gastric fluid. (Blondlot, xvi.)

*Magnesium* appears to be always associated with calcium, and probably exists in the same forms as it; but its proportion is always much smaller, except in the juice expressed from muscles, in the ashes of which magnesia preponderates over lime. (Liebig, liv.)

*Iron.*—The especial place of iron is in the hæmatosine, the colouring-matter of the blood, of which a further account will be given with the chemistry of the blood. Peroxyde of iron is found, in very small quantities, in the ashes of bones, muscles, and many tissues, and of lymph and chyle, albumen of serum, fibrine, bile, and other fluids; and a salt of iron, probably a phosphate, exists in considerable quantity in the hair, black pigment, and other deeply coloured epithelial or horny substances.

*Manganesium.*—Vauquelin believed he found a trace of the peroxyde of this metal in the ashes of hair and bones; but in the more accurate analysis of the former substance by V. Laer, and of the latter by V. Bibra, no mention of manganesium is made. It has been detected in gall-stones (lxxxii. vol. i. p. 4). According to M. E. Millon (xviii. 1848), it exists naturally in blood: and M. Burin du Buisson (clx. Fevrier, 1852) confirms this observation, and states his belief that it belongs solely to the corpuscles, and not to the serum. Glenard, however, believes that it is an accidental and not a constant ingredient in the blood (lix. 1855, p. 112).

*Aluminium* also is stated (Henle, xxxvii. p. 4) to exist in the ashes of hair, bones, and enamel; but neither V. Laer nor V. Bibra mentions it.

*Copper.*—After long disputes, the general existence of copper in the human liver may be regarded as proved by the experiments of Orfila, Heller, and others. It exists in especially large quantity in dark biliary calculi; and we may probably assume, that it does not enter into the proper permanent

substance of the liver, but is contained in the bile, within the bile-cells and ducts, and is destined with it to be excreted. It is true, that Harless and V. Bibra have found it constantly present in the blood, as well as in the liver, of many Mollusca and fish: and that in their blood it takes the place of some proportion of the iron contained in the blood of other species, and may be regarded as a normal, necessary constituent; yet, it seems most likely that, in the human body, both copper, manganesium, and aluminium are merely *accidental elements*, which, being taken in minute quantities with the food, and not excreted at once with the fæces, are absorbed and deposited in some tissue or organ, of which, however, they form no necessary part. In the same manner, arsenic and lead, being absorbed, may be deposited in the liver and other parts. This view is confirmed by the fact observed by Heller, that although copper is frequently present in the bile of adults, yet it is never found in that of infants (ix. vol. ii. p. 321). The researches of Cattanei di Momo also seemed to prove, that neither copper nor lead exists in the bodies of new-born children or infants (xxv. 1843-4, p. 3).

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## CHAPTER II.

### STRUCTURAL COMPOSITION OF THE HUMAN BODY.

THE component substances of the body are commonly divided into fluids and solids.

The *fluids* are, 1st, *formative fluids*, from which are derived the materials for the formation of the solid tissues; and, 2nd, *secreted fluids*, which are separated from the tissues and the blood, through, speaking generally, the operation of special organs, such as cells arranged in glands or membranes.

So little can be said that would apply to all the members of either of these classes of the fluids, that a general description of them would be useless; they will therefore be considered

in their several more appropriate places.—[See chapters on BLOOD, LYMPH, CHYLE, the several SECRETIONS, etc.]

Among the *solids* of the body, some appear, even with the help of the best microscopic apparatus, perfectly uniform and simple: they show no trace of structure, *i.e.*, of being composed of definitely arranged dissimilar parts. These are named *simple, structureless,* or *amorphous solids.* Such are the apparently structureless mass composing the albumen of eggs, and the substance called *cytoblastema*, or *formative substance*, in which the nuclei and cells are imbedded in many tissues in progress of development. Such also is the simple membrane which forms the walls of most primary cells, of the finest capillary blood-vessels and gland-ducts, and of the sarcolemma of muscular fibre; and such is the membrane enveloping the vitreous humour of the eye. Such also, having a dimly granular appearance, but no really granular structure, is the intercellular substance of the most perfect cartilage.

In the solids which present determinate structure, certain primary forms may be distinguished, which, by their various modifications and modes of combination make up the tissues and organs of the body. Such are, 1. *Granules* or *molecules*, the simplest and minutest of the primary forms. They are particles of various size, from immeasurable minuteness to the 10,000th of an inch in diameter; of various and generally uncertain composition, but usually so affecting light transmitted through them, that at different focal distances their centre, or margin, or whole substance, appears black. From this character, as well as from their low specific gravity (for in microscopic examinations they always appear lighter than water), and from their solubility in ether when they can be favourably tested, it is probable that most granules are formed of fatty or oily matter; or, since they do not coalesce as minute drops of oil would, that they are particles of oil coated over with albumen deposited on them from the fluid in which they float. (See Ascherson, lxxx. 1848). In any fluid that is not too viscid, they exhibit the phenomenon of *molecular motion*, shaking and

vibrating incessantly, and sometimes moving through the fluid, probably under the influence of external vibration.

Granules are either *free*, as in milk, chyle, milky serum, yelk-substance, and most tissues containing cells with granules; or *enclosed*, as are the granules in nerve-corpuscles, gland-cells, and epithelium-cells, the pigment granules in the pigmentum nigrum and medullary substance of the hair; or *imbedded*, as are the granules of phosphate and carbonate of lime in bones and teeth.

2. *Nuclei*, or *cytoblasts*, appear to be the simplest elementary structures, next to granules. They were thus named in accordance with the hypothesis that they are always connected with cells, or tissues formed from cells, and that in the development of cells, each nucleus is the germ or centre around which the cell is formed. The hypothesis is only partially true, but the terms based on it are too familiarly accepted to make it advisable to change them till some more exact and comprehensive theory is formed.

Of the corpuscles called nuclei, or cytoblasts, the greater part are minute cellules or vesicles, with walls formed of simple membrane, enclosing a colourless pellucid fluid, and often one or more particles, like minute granules, called *nucleus-corpuscles*, or *nucleoli*. Such vesicular nuclei, without nucleoli, are those of the blood-corpuscles of oviparous vertebrate animals (pl. i., fig. 2 and 3); and such, with nucleoli, are those of epithelium-cells and pigment-cells. But some nuclei appear to be formed of an aggregate of granules imbedded in a pellucid substance; as, for example, the nuclei of the lymph and chyle-corpuscles.

The composition of the nucleus is uncertain. One of its most general characters, and the most useful in microscopic examinations, is, that it is neither dissolved nor made transparent by acetic acid, but acquires, when that fluid is in contact with it, a darker and more distinct outline.

Nuclei may be either *free* or *attached*. *Free nuclei* are such as either float in fluid, like those in the gastric juice, which appear to be derived from the secreting cells of the gastric

glands, or lie loosely imbedded in solid substance, as in the grey matter of the brain and spinal cord, and most abundantly in some quickly-growing tumours.

*Attached nuclei* are either closely imbedded in homogeneous pellucid substance, as in rudimental cellular tissue; or are fixed on the surface of fibres, as on those of organic muscle (plate ii., fig. 9, A.) and organic nerve-fibres; or are enclosed in cells, or in tissues formed by the extension or junction of cells. Nuclei enclosed in cells appear to be attached to the inner surface of the cell-wall, projecting into the cavity. Their position in relation to the centre or axis of the cell is uncertain; often, when the cell lies on a flat or broad surface, they appear central, as in blood-corpuscles, epithelium-cells, whether tessellated or cylindrical; but, perhaps, more often their position has no regular relation to the centre of the cell. In most instances, each cell contains only a single nucleus; but in cartilage, especially when it is growing or ossifying, two or more nuclei in each cell are common; and the development of new cells is often effected by a division or multiplication of nuclei in the cavity of a parent cell; as in primary blood-cells, the germinal vesicle, and others.

When cells extend and coalesce, so that their walls form tubes or sheaths, the nuclei commonly remain attached to the inner surface of the wall. Thus they are seen imbedded in the walls of the minutest capillary blood-vessels of, for example, the retina and brain; in the sarcolemma of transversely striated muscular fibres; and in minute gland-tubes. In such cases, their arrangement may be irregular, as in the capillaries; or regular, as in the single or alternating double rows of nuclei in different examples of the muscular fibre.

Nuclei are most commonly oval or round, and do not generally conform themselves to the diverse shapes that the cells assume; they are, altogether, less variable elements, even in regard to size, than the cells are; of which fact one may see a good example in the uniformity of the nuclei in cells so multiform as those of epithelium. But sometimes they appear to

be developed into filaments, elongating themselves and becoming solid, and uniting end to end for greater length, or by lateral branches to form a network. So, according to Henle (xxxvii. p. 194), are formed the filaments of the striated and fenestrated coats of arteries, and the yellow or elastic filaments that are mingled with the common filaments of cellular tissue, and with organic muscular fibre, especially in the walls of arteries. The filaments of the cortical substance of hair, and the seminal filaments, or spermatozoids, appear to be also elongated and divided nuclei.

3. *Cells*, *Primary cells*, or *Elementary cells*, are vesicles or scales of larger average size than nuclei, but, like them, composed, in the normal state, of membranous cell-walls, with, usually, liquid contents, and generally round or oval.

The cell-wall never presents any appearance of structure: it appears sometimes to be a proteine-substance, as in blood-cells; sometimes a horny matter, as in thick and dried cuticle. In almost all cases (the dry cells of horny tissue, perhaps, alone excepted) the cell-wall is made transparent by acetic acid, which also penetrates through it and distends it, so that it can hardly be discerned. But in such cases the cell-wall is usually not dissolved; it may be brought into view again by merely neutralising the acid with soda or potash.

In some instances, the most developed state of the cell is that in which it has no nucleus, as in the mammalian blood-corpuscles, in which, as will be described, the substance of the nucleus of the lymph or chyle-corpuscle is gradually all appropriated and changed to the contents of the blood-corpuscle.

But, in other instances, especially in old cells, as in those of the nails, the outer layers of epidermis, and the adipose tissue, the nucleus may disappear, wasting away; and this is, probably, always a sign of degeneration of the tissue, for a similar wasting of nuclei is commonly observed in all tissues in the state of fatty degeneration.

With the exceptions just mentioned, all the cells of the human body appear to contain nuclei. Sometimes the nucleus

nearly fills the cavity of the cell, as in lymph and chyle-corpuscles, in which the cell-wall lies so close round the nucleus, that it can hardly be seen till it is raised up by water or acetic acid insinuating itself between it and the nucleus; and such is the proportion between the nucleus and cell in young epidermis-cells; but more often the nucleus has a diameter from one-fourth to one-tenth less than that of the cell.

The simplest *shape* of cells, and that which is probably the normal shape of the primary cell, is oval or spheroidal, as in cartilage-cells and lymph-corpuscles; but in many instances they are flattened and discoid, as in the blood-corpuscles, or scale-like, as in the epidermis and tesselated epithelium. By mutual pressure they may become many-sided, as most of the the pigment cells of the choroidal pigmentum nigrum and in close-textured adipose tissue; they may assume a conical or cylindriform or prismatic shape, as in the varieties of cylinder-epithelium and the enamel-tubes; or be caudate, as in certain bodies in the spleen; they may send out exceedingly fine processes in the form of vibratile cilia, or larger processes, with which they become stellate, or variously caudate, as in the large nerve- or ganglion-corpuscles, and the epithelium of the choroid plexuses.

The *contents* of cells, including under this term all but their nuclei, are almost infinitely various, according to the position, office, and age of the cell. In adipose tissue they are the oily matter of the fat, the mixture of margarine and oleine; in gland-cells, the contents are the proper substance of the secretion, bile, semen, etc., as the case may be; in pigment-cells they are the pigment granules that give the colour; and in the numerous instances in which the cell-contents can be neither seen because they are pellucid, nor tested because of their minute quantity, they are yet, probably, peculiar in each tissue, and constitute the greater part of the proper substance of each. Commonly, when the contents are pellucid, they contain granules which float in them; and when water is added and the contents are diluted, the granules display an

active molecular movement within the cavity of the cell. Such a movement may be seen by adding water to mucus-, or granulation-corpuscles, or to those of lymph. In a few cases, the whole cavity of the cell is filled with granules: it is so in yelk-cells and milk-corpuscles, in the large diseased corpuscles often found among the products of inflammation, and in some cells when they are the seat of extreme fatty degeneration. All cells containing abundant granules appear to be either lowly organized, as for nutriment, *e. g.*, yelk-cells, or degenerate, *e. g.*, granule-cells of inflammation, or of mucus. The peculiar contents of cells may be often observed to accumulate first around or directly over the nuclei, as in the cells of black pigment, in those of melanotic tumours, and in those of the liver during the retention of bile.

*Intercellular substance* is the material in which, in certain tissues, the cells are imbedded. Its quantity is very variable. In the finer epithelia, especially the columnar epithelium on the mucous membrane of the intestines, it can be just seen filling the interstices of the close-set cells; here it has no appearance of structure. In cartilage and bone, it forms a large portion of the whole substance of the tissue, and is either homogeneous and finely granular, or osseous, or, as in fibro-cartilage, resembles tough tendinous tissue. In some cases, the cells are very loosely connected with the intercellular substance, and may be nearly separated from it, as in fibro-cartilage: but in some their walls seem amalgamated with it.

The foregoing may be regarded as the simplest, and the nearest to the primary, forms assumed in the organization of animal matter; as the states into which it passes in becoming a solid tissue living or capable of life. By the further development of tissue thus far organized, according to rules which will be hereafter described, higher or secondary forms are produced which it will be sufficient in this place merely to enumerate. Such are, 4, *Filaments*, or *fibrils*.—Threads of exceeding fineness, from $\frac{1}{20000}$th of an inch upwards. Such filaments are either cylindriform, as are those of the striated muscular

(pl. ii. fig. 7 and 8) and the fibro-cellular or areolar tissue (pl. ii. fig. 4); or flattened, as are those of the organic muscles (pl. ii. fig. 9), the common elastic tissue (pl. ii. fig. 3) and the finer variety of the same tissue, which is commonly associated with the proper white filaments of the fibro-cellular tissue. Filaments usually lie in parallel fasciculi, as in muscular and tendinous tissues; but in some instances are matted or reticular with branches and intercommunications, as are the filaments of the middle coat, and of the longitudinally-fibrous coat of arteries; and in other instances, are spirally wound, or very tortuous, as in the common fibro-cellular tissue.

5. *Fibres*, in the instances to which the name is commonly applied, are larger than filaments or fibrils, but are by no essential general character distinguished from them. The flattened band-like fibres of the coarser varieties of organic muscles and elastic tissues are the simplest examples of this form; the toothed fibres of the crystalline lens are more complex; and more compound, so as hardly to permit of being classed as elementary forms, are the striated muscular fibres, which consist of bundles of filaments enclosed in separate membranous sheaths, and the cerebro-spinal nerve-fibres in which similar sheaths inclose apparently two varieties of nerve-substance.

6. *Tubules* are formed of simple membrane, such as the minute capillary lymph- and blood-vessels, the investing sheaths of striated muscular and cerebro-spinal nerve-fibres, and the basement membrane or proper wall of the fine ducts of secreting-glands.

Most of the tissues which are composed of these primary structures will be briefly described in future chapters, and in connection with the physiology of the organs that they help to form. The insertion of a system of general anatomy would not further the purpose of this work; and would be superfluous while the student has access to such admirable works devoted to the subject as the Introduction to Quain's Anatomy by Dr. Sharpey, the Physiological Anatomy of Dr.

Todd and Mr. Bowman, Kölliker's Manual of Human Histology, translated for the Sydenham Society, and his recently published work, a Manual of Human Microscopic Anatomy, the Microscopic Anatomy of the Human Body by Dr. Hassall, and the various articles on the tissues published in the Cyclopædia of Anatomy and Physiology.

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## CHAPTER III.

### VITAL PROPERTIES OF THE ORGANS AND TISSUES OF THE HUMAN BODY.

Some of the actions observed in living bodies indicate the operation of other properties and forces besides those which can be referred to the chemical and mechanical constitution of organized substances. These properties being the sources of phenomena which are peculiar to living beings, are named *vital properties;* the forces issuing from them, *vital forces;* the acts in which they are expressed, such as those enumerated at pp. 1, 2, are *vital acts* or *vital processes:* and the state in which these processes are displayed is *life.*

1. The most general, perhaps an universal, property of living bodies, is that which is manifested in the ability to form themselves out of materials dissimilar from them; as when, for example, the ovule develops itself from the nutriment of the fluids of the parent,—or when a plant, or any part of one, grows by appropriating the elements of water, carbonic acid, and ammonia,—or when an animal subsists on vegetables, and its blood and various organs are formed from the materials of its food. The force which is manifested in these acts is termed *formative force* (assimilative, or plastic force); and the processes effected by it are named *assimilative, nutritive,* or *formative processes.*

This power of self-formation from dissimilar materials, which

appears to be wholly peculiar to living bodies, and without which, probably, none exists, manifests itself in three modes, which, though they bear different names, yet, probably, are only three expressions of one force operating in different conditions: they are *development*, *growth*, and *assimilation*, or *maintenance*.

Development is the process by which each tissue or organ of a living body is first formed; or by which one, being already incompletely formed, is so changed in shape and composition as to be fitted for a function of a higher kind; or, finally, is advanced to the state in which it exists in the most perfect condition of the species.

Growth, which commonly concurs with development and continues after it, is, properly, mere increase of a part by the insertion or super-addition of materials similar to those of which it already consists. In growth, properly so called, no change of form or composition occurs: parts only increase in weight and, usually, in size; and if they acquire more power, it is only more power of the same kind as that which they before enjoyed.

In assimilation, or self-maintenance, living bodies preserve their condition, notwithstanding the changes to which they are liable through the influence of external forces and their own natural decay; and the stability of composition which they thus display is effected by the continual formation of new particles in the place of those that are impaired and removed.

The modes in which these three manifestations of formative power are accomplished, will be considered hereafter, especially in the chapters on NUTRITION, SECRETION, and DEVELOPMENT. From these it will appear, that the most general, and one of the simplest modes, is in the formation and further development of nucleated cells. The nucleated cell is the form towards which organising matter most commonly tends, in which it often rests, and through which it usually proceeds in its further developments. In nucleated cells, also, are the best examples of inherent formative power, which, not being consumed in the formation of the cells, remains operative in them, changing them and

their contents, and influencing the surrounding or intercellular substance in which they are deposited. Thus, whether it be for the preparation of materials from food which may serve to the maintenance of the body, or for the construction of the several tissues, or for the formation or temporary storing-up of the materials that are to be removed from the body as refuse, in all these, and in nearly all instances of them, the end is attained by or with the help of the formation, continued energy, or dissolution of nucleated cells.

The property to which is referred the formative power of living beings, or living parts, is, however, no simple property, such as the "attraction" of mechanical science, or the "affinity" of chemistry. These manifest themselves in acts so simple and almost uniform, that the hypothesis which assumes the existence of such properties, supplies at once the language in which their laws of action may be enunciated. But in the simplest exercise of living formative power, even in that which accomplishes the formation of a cell, there is evidence of the operation of many forces. Mechanical force is shown in the determination of the position, shape, and relations of the cell; chemical force, in the determination of the composition of its walls and contents: and with these, or as if directing them, that vital force, different from them and from all other known physical forces, is in operation, by virtue of which the cell acquires all the properties that characterise the species or organ to which it is attached, and becomes capable of taking part in vital processes—even in such processes as those in which itself originated.

Thus the vital formative force seems not to oppose or exclude, but to include and direct the physical forces that issue from the mere matter of the organic body. It may, therefore, be believed that every vital act is accompanied with physical changes in the active matter: but there is no sufficient evidence that such changes ever wholly constitute or make up any of those that are commonly called vital acts. In all those acts or processes some force is exercised peculiar to the state

of life, and as different from all recognised physical forces as they are different from one another. We cannot tell how much in each act of the living body is physical, and how much depends on the peculiar vital force. The advancing knowledge of the physical sciences does, indeed, prove every year that effects, which used to be ascribed to vital forces, are due to the operation of the forces of chemistry and mechanics, and it may be observed, generally, that the substances in which the processes of organic life are most actively carried on are those whose chemical composition is most remote from that of inorganic matter. Still, many things yet remain, observed only in the living body, so completely dependent on the maintenance of the whole state of life, and so different from what physical forces ever accomplish in dead matter, that we cannot refer them to the operation of those forces. Any hypothesis which would abolish the idea of vital formative force, would be much less reasonable and useful than that which admits it; indeed, unless we admit the existence of such a force in the processes of organic life, and adopt the language which the hypothesis suggests, it is hardly possible to express the ordinary facts of physiology.

2. *Contractility* may be reckoned a second vital property. It consists in the power which certain tissues have, during life, of contracting or shortening themselves in a peculiar manner. Such contractility is usually and best observed in fibrous tissues, as in the muscles of organic and animal life; but it may be seen, also, in cells and collections of them, as in the muscles of embryoes, while they yet consist of cells, and before any fibres are developed in them.

The peculiar contraction of muscular and other organic tissues differs from the contraction of which dead and inorganic matter is capable, both in its modes and in the conditions that give rise to it. The modes of contraction will be described hereafter: the conditions are not only such previous elongation as would be followed by contraction in any elastic body, but also various slight changes, such as those produced by the

contact of foreign matters, variations of temperature, electricity, etc. These, and whatever will give rise to the peculiar contractions in the organic tissues, are called *stimuli.*

That which most characterises the contractility of animal tissues is, that the contraction may be excited by the application of a stimulus to the nerves that ramify in them; and, indeed, it is generally through the nerves that the stimulus which produces a contraction is conveyed. In the chapter on the MUSCLES it will be shewn, that the property of contractility is inherent in the tissues that contract, and is essentially independent of their nerves; so that contraction *may* take place without the co-operation of the nerves. Therefore, the whole property of *irritability*, including both the capacity of receiving a direct stimulus and the power of contracting in consequence thereof, may be ascribed to the muscles and other contractile tissues. But, in the ordinary conditions of life, the nerves may be said to be necessary to contractions, because, in these conditions, it is only through the medium of nerves that a stimulus is applied to the contractile tissues; and when the nerves are destroyed contractions do not naturally ensue.

The modes in which stimuli are applied to, and their effects conveyed along, nerves to the contractile parts, will be described in the chapter on the NERVOUS SYSTEM. One mode is essentially characteristic of animals; that, namely, wherein the contractile tissues are made to act by a Mind, an *Anima;* which, having knowledge of the existence of the body, consciousness of power and will to exercise it, acts on the nervous system,* and through it on the contractile tissues: thus voluntary motion is produced.

3. The *power of conducting* or *transmitting* stimuli or im-

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* It does so, at least, in all animals in which a nervous system can be demonstrated. In those in which none has been yet seen, it must be doubtful whether the mind can directly influence the contractile tissues, or whether some nervous material exists which we cannot discover, but through which the mind of the animal can act.

pressions which, in the foregoing paragraphs, has been ascribed to the nerves, constitutes another peculiar vital property. It belongs to the nervous system alone, and may be said to consist in this—that the state, or change, which is produced in the fibre of a nerve by the application of a stimulus of any kind, may be propagated through the whole length of the fibre, so that every part thereof shall, with immeasurable rapidity, be brought into the same state as the part first stimulated. Thus the stimulus, or rather the change or *impression* produced by it, is said to be *conducted* by the nerve; in the same way as it is said electricity is conducted along a wire, although at the instant of contact with the source of electricity the whole wire becomes at once electric.

A peculiar force is generated by the change thus produced in nerves, the effect of which force, when the nerve conveys it to a muscle, is shewn by the muscle contracting with a force which, other things being equal, is directly proportionate to the intensity of the stimulus. The same force, generated by stimulating nerves, may also be shewn by changes in organic processes; as when secretions are augmented, diminished, or altered, in states of nervous excitement. The force thus developed in the nerves has been named *vis nervosa;* but there is an objection to the use of the term, since some appear to think that force is exercised only when the conduction takes place towards muscles, and that in that case the force itself is in some way transferred from the nerves to the muscle. But a safer hypothesis appears to be that which holds that a peculiar force is generated whenever a nerve is stimulated; and which ascribes to all nerves alike the power of conducting impressions; *i. e.*, of propagating the changes produced by stimuli, and the force issuing therefrom. Adopting this hypothesis, we may believe that the different consequences of such conducted force depend on the various connections of the conducting nerve-fibres with the nervous centres and contractile parts, on the nature and strength of the stimulus, and on other circumstances external to the nerves.

When an impression is conveyed from any part of the body, along a nerve, to the brain, the mind may take cognizance of it: what the mind thus becomes conscious of is called a *sensation;* and the act of the mind noticing it, *perception;* and all parts through the nerves of which such sensations may be derived are called sensible or sensitive parts. But in the use of the latter term, it must be remembered, that they mean only that certain parts are capable of giving rise to sensations. The mind alone is sentient and percipient; neither tissues, nerves nor brain, could of themselves, or from any property or change of which they are capable, become in any sense conscious of their condition.

Such appear to be the peculiar properties of living animal matter. It is all capable of self-formation, and the various modes of formation constitute the principal functions of the organic life of the animal. Some of the living tissues are, also, capable of peculiarly contracting; and the nervous tissue is capable of peculiarly conducting the changes or impressions made on it by certain stimuli. These two properties, in their various modifications, are exercised especially in the animal life, and it is by means of these, that the mind becomes cognizant of the condition of the body, and through it, of some of the properties of things that act on it, as well as able to will the movements of its several parts.

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## CHAPTER IV.

### THE BLOOD.

THE processes enumerated in the first division of the phenomena of Organic Life have their end or purpose in the forma-

tion, movement, and purification of the blood. The physiology of the blood must, therefore, precede the consideration of these subservient processes.

Wherever blood can be seen as it flows in the vessels of a living part, it appears a colourless fluid containing minute particles, the greater part of which are red, and give the blood its colour. The fluid is named *liquor sanguinis;* the particles are the *blood and lymph-corpuscles*, or *cells.*

When blood flows from the living body, it is a thickish heavy fluid, of bright scarlet colour when it comes from an artery; deep purple, Modena, or nearly black, when it flows from a vein. Its specific gravity at 60° F. is, on an average, 1055, that of water being reckoned as 1000; the extremes consistent with health being, according to Nasse, 1050 and 1059 (xv. vol. i. p. 82). Its temperature is, generally, about 100° F., that of blood in the left side of the heart being 1° or 2° higher than that in the right (Savory, ccxx.); it has a slight alkaline reaction; and emits an odour similar to that which issues from the skin or breath of the animal from which it flows, but fainter.

The above-mentioned *differences of colour* in arterial and venous blood, are sometimes not to be observed. If blood runs very slowly from an artery, as from the bottom of a deep and devious wound, it is generally as dark as venous blood. In persons nearly asphyxiated, also, and sometimes under the influence of chloroform or ether, the arterial blood becomes like the venous. But in all these cases, the dark blood becomes bright on exposure to the air. Bernard has lately shewn that venous blood returning from a gland in active secretion is almost as bright as arterial blood (ccxxviii. No. iv. p. 649).

The *specific gravity* of men's blood is, on an average, rather greater than that of women's, because of the larger proportion of red-corpuscles in the former; that of robust persons, for the same reason, is greater than that of the feeble. It is always diminished by bleeding; and so quickly, that in a single venesection the specific gravity of a portion of the blood last drawn

is often less than that of the blood that flows first (J. Davy, lxxxv. vol. ii. p. 28: Polli, xci.) The specific gravity of blood is increased in diseases attended with great watery discharges, as cholera and diabetes; but with these exceptions, a specific gravity above the natural standard would generally indicate a disease attended with plethora, or excess of the animal constituents of blood, and a low specific gravity, a disease of debility or exhaustion.

The *alkaline reaction* appears to be a constant character of blood in all animals and under all circumstances. An exception has been supposed to exist in the case of menstrual blood; but the acid reaction which this sometimes presents is due to the mixture of an acid mucus from the uterus and vagina. Pure menstrual blood, such as may be obtained with a speculum, or from the uteri of women who die during menstruation, is always alkaline, and resembles ordinary blood (Whitehead, lxxxvi.) According to Bernard, blood becomes spontaneously acid after removal from the body, owing to conversion of its sugar into lactic acid (ccxiv. Ap. 21, 1860.)

The *odour* of blood is easily perceived in the watery vapour, or *halitus* as it is called, which rises from blood just drawn: it may also be set free, long afterwards, by adding to the blood a mixture of equal parts of sulphuric acid and water. It is said to be not difficult to tell, by the likeness of the odour to that of the body, the species of domestic animal from which any specimen of blood has been taken: the strong odour of the pig or cat, and the peculiar milky smell of the cow, are especially easy to be thus discerned in their blood (Barruel, lxxxvii. No. 1.)

There is still such wide discrepancy in the statements of different observers, respecting the total *quantity* of blood in the body, that no positive opinion on the subject can yet be given. According to the majority of authors, it is about equal to from one-fifth to one-eighth of the weight of the whole body, though recent experiments seem to show that this estimate is much too high.

### *Coagulation of the Blood.*

When blood is drawn from the body, and left at rest, certain changes ensue which constitute a kind of rough analysis of it, and are instructive respecting the nature of some of its constituents. After about ten minutes, taking a general average of many observations, it gradually clots or coagulates, becoming solid like a soft jelly. The clot thus formed has at first the same volume and appearance as the fluid blood had, and, like it, looks quite uniform: the only change seems to be that the blood which was fluid is now solid. But presently, drops of transparent yellowish fluid begin to oose from the surface of the solid clot; and these gradually collecting, first on its upper surface, and then all around it, the *clot*, or "*crassamentum*," diminished in size, but firmer than it was before, floats in a quantity of yellowish fluid, which is named *serum*, and the quantity of which may continually increase for from twenty-four to forty-eight hours after the clotting of the blood.

The changes just described may be thus explained. The *liquor sanguinis*, or liquid part of the blood, consists of serum, holding fibrine in solution. The peculiar property of fibrine, as already said (p. 13), is its tendency to become solid when at rest, and in some other conditions. When, therefore, a quantity of blood is drawn from the vessels, the fibrine, being (in the normal state) equally diffused through the whole mass, coagulates, and serum and blood corpuscles are held, or, as it were, soaked and entangled in the solid substance which it forms.

But after healthy fibrine has thus coagulated, it always contracts; and what is generally described as one process of coaglation should rather be regarded as consisting of two parts or stages; namely, first, the simple act of clotting, coagulating, or becoming solid; and, secondly, the contraction or condensing of the solid clot thus formed. By this second act, much of the serum which was soaked in the clot is gradually pressed out; and this collects in the vessel round the contracted clot.

Thus, by the observation of blood within the vessels, and of the changes which commonly ensue when it is drawn from them, we may distinguish in it three principal constituents, namely, 1st, the fibrine, or coagulating substance, which has been also called the lymph, or coagulating lymph, of the blood; 2nd, the serum, in which the fibrine, before its coagulation, was dissolved; 3rd, the blood and lymph corpuscles.

That the fibrine is the only spontaneously coagulable material in the blood, may be proved in many ways; and, most simply by employing any means whereby a portion of the liquor sanguinis, *i.e.*, the serum and fibrine, can be separated from the red corpuscles before coagulation. This separation is always effected when coagulation is retarded beyond the usual time, or when the red corpuscles, which have a higher specific gravity than the other constituents of the blood, sink more rapidly than usual. Coagulation may be retarded by cold, or by drawing the blood into a vessel containing oil, so that as the oil floats over it, it may be excluded from the air. The red corpuscles also, sink quickly in blood drawn from patients with inflammatory diseases, and in horses' blood. In any of these cases the red corpuscles may be observed, while the blood is yet fluid, to sink below its surface; and the layer beneath which they have sunk, and which has usually an opaline or greyish-white tint, will coagulate without them, and form a white clot consisting of fibrine alone, or of fibrine with entangled white corpuscles; for the white corpuscles, being very light, tend upwards towards the surface of the fluid. The layer of white clot which is thus formed rests on the top of a coloured clot of ordinary characters, *i.e.*, of one in which the coagulating fibrine has entangled the red corpuscles while they were sinking: and, thus placed, it constitutes what has been called a *buffy coat*.

It is also by the action of the fibrine alone that the contraction of the clot is effected, and the contraction is greatest when it is least hindered by particles enclosed in the solid fibrine. Hence, when a buffy coat is formed in the manner just described, it commonly contracts more than the rest of the clot

does, and, drawing in at its sides, produces that *cupped* appearance on the top of the clot which is often characteristic of the existence of inflammation.

It is thus evident that the coagulation of the blood is due to its fibrine. We are not yet able to explain certainly why fibrine coagulates; but the hypothesis hitherto most generally entertained is, that its coagulation is a process of organization —a spontaneous assumption of organic form and structure which, in favourable conditions, would be the first step towards the formation of a more highly organized tissue. The principal evidence adduced for this view is as follows:—

1.—When the coagulation of fibrine is observed with the microscope (and this may be easily done in a minute portion of liquor sanguinis taken when the red corpuscles are subsiding) it appears, when first solidified, soft and quite homogeneous; but gradually, when it becomes tougher, it acquires the appearance of a closely matted or felt-like mass of fine white pliant fibrils, in which scattered granules and white corpuscles are imbedded. Such a filamentous structure, with filaments separable by minute dissection, is observable in all well-formed fibrine clots, and is characteristic of organization; at least, such structures are not seen in inorganic matter, or in organic matter artificially coagulated as albumen; but they are found in the more lowly organized tissues, such as that of the membrane of egg-shell (Carpenter, xciii. 1844, p. 1), organizing lymph, some of the least developed tumours, etc.

2. The coagulation of fibrine is hardly, if at all, distinguishable from that of lymph effused in inflammation. Both alike spontaneously coagulate in the same mode, and acquire the same simple structure; both alike contract after coagulation; and generally, when lymph effused in any case of inflammation has little tendency to organization, the fibrine of the patient's blood coagulates very weakly and imperfectly. It is on the whole probable that the lymph of inflammatory effusion is the fibrine of the blood only somewhat modified by the disease. But the lymph, after coagulating, goes on to more perfect or-

ganization, and becomes a vascular tissue; the fibrine shews no such further change, at least in blood drawn from the body. Yet, seeing that the coagulation of the lymph is the first step in its organization, it has been thought reasonable to regard the similar change in the fibrine as also organization, and to explain the subsequent difference between them by the difference of their external conditions. The lymph continues to be organized, being placed among living organizing parts that may supply it with the necessary materials for its support; the fibrine does not so continue, having none of these, perhaps essential advantages.

3. The coagulation of blood out of the body is not different from its coagulation, under certain conditions within the body, as, *e.g.*, when the circulation through a vessel is obstructed by a ligature, or when blood is effused from its vessels into an adjacent cavity or tissue. And there is sufficient evidence that, in many cases, when the blood thus coagulates in contact with healthy living tissues, its coagulation is the first step towards a more complete organization, and the formation of vascular tissue; just as the coagulation of the lymph effused in inflammation is the beginning of its complete organization. The instances in which this organization of blood, or rather of the fibrine of blood, has been best observed, are those in which the blood coagulates above a ligature of an artery, and forms there what is called the *conical clot*. Such a clot gradually loses its colour by the disintegration of the red corpuscles. By the absorption of its serum, it becomes firmer and drier; then it acquires the structure of fine filamentous tissue, and a supply of blood-vessels; it is more and more intimately united with the walls of the vessel, and at length forms part of the fibrous cord by which, finally, the obliterated portion of the artery is replaced. In this process, which has been minutely examined by Zwicky (lxxxix.), the changes through which the fibrine of the blood passes are, in all essential respects, similar to those which constitute the organization of lymph into false membrane or adhesions. Doubtless, the process is similar by which effused

blood is, in many other cases, organized; as, for example, in apoplexy of the cerebral membranes, in which a thin layer of blood, having coagulated, may be traced through stages of organization till it is nearly all formed into a tough membrane lining the dura mater; or in which, when the effusion of blood is more abundant, a layer on the surface of the clot may form a sac or cyst of finer membrane, vascular and transparent like the arachnoid, and enclosing the rest of the blood (see especially Dr. Burrows, lxxi. 1835; and Mr. P. Hewett, xli. 1845). Such organization of clots of blood is also seen in certain tumours attached to the interior of the heart, and more rarely of the arteries, as well as in the formation of phlebolithes, or vein-stones, and of the cords by which veins after slight phlebitis, as in phlegmasia dolens, are often obstructed or obliterated.*

Such is the principal evidence for ascribing the coagulation of blood to the organisation of the fibrine, and for adhering to Mr. Hunter's view, that "coagulation is an operation of life" (i. vol. iii. n. 34); for here he used the term "life" in the same sense as that in which one speaks of a live egg, or a live seed, implying not an active state of life, but the capacity of developing and acquiring higher organisation in conditions favourable to life. And the fact, that the coagulation of blood may be suspended for any length of time by freezing it, or by adding to it large quantities of alkaline salts, is said to be no more a disproof of Mr. Hunter's doctrine than the fact, that eggs are not developed except at a certain temperature, is a proof that they are incapable of development. It is considered that nothing more is proved by such a fact, than that certain external conditions are necessary for the perfect performance of these as of all other "operations of life."

Against this doctrine, that coagulation is a vital act, there

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* Most Museums contain such specimens. In the Museum of the Royal College of Surgeons, Nos. 12, 1528, 1732, 1733, 1742, may be referred to: in that of St. Bartholomew's Hospital, Nos. 1 and 3 in Series vi., 107 in Series xiii., 45 and 49 in Series xiv.

has, however, of late been brought forward a large amount of evidence, which, if not quite sufficient to overturn it, is yet enough to throw great doubt on its correctness. According to the modern views founded on such evidence, and supported by many distinguished physiologists and pathologists, coagulation, instead of being an "operation of life," is really an indication of the death of the fibrine,—a physical assumption of the solid form in consequence of its being removed from the influence of living parts, and not the first step in a process of organization. The solidification of the fibrine is, according to this view, analogous to the coagulation of albumen by heat, or the gelatinization of a solution of gelatine on cooling.

Whatever view is taken of the process of coagulation, the fact that fibrine admits of being organized when placed in favourable conditions, must not, however, be regarded as evidence that any of the tissues are naturally constructed out of this material, or that fibrine is a compound of higher grade than albumen, and one through which albumen must pass before it is assimilated by the tissues: for there is no evidence that this is so, while there is much that fibrine is a substance lower in the scale of organic principles than albumen, which, in all cases, seems to be essential to nutrition.

### *Conditions affecting Coagulation.*

Although the coagulation of fibrine is spontaneous, yet it is liable to be modified by the conditions in which it is placed, such as temperature, motion, the access of air, the substances with which it is in contact, the mode of death, etc. All these conditions need to be considered in the study of the coagulation of the blood.*

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* The fullest accounts of them all are given by Nasse (xv. vol. i. Art. *Blut*), Gulliver in his Edition of Hewson's works for the Sydenham Society, and, especially, Dr. Richardson, in his Prize Essay on the Cause of the Coagulation of the Blood: see also Brücke (cxc. vol. xxxvii.)

*Cold* retards the coagulation of blood; and it is said that, so long as blood is kept at a temperature below 40° F., it will not coagulate at all. Freezing the blood, of course, prevents its coagulation; yet it will coagulate, though not firmly, if thawed after being frozen; and it will do so, even after it has been frozen for several months. Coagulation is accelerated, but the subsequent contraction of the clot is hindered, by a temperature between 100° and 120°: a higher temperature retards coagulation, or, by coagulating the albumen of the serum, prevents the coagulation of the fibrine.

*Rest* is favourable to the coagulation of blood. Blood, of which the whole mass is kept in uniform motion, as when a closed vessel completely filled with it is constantly moved, coagulates very slowly and imperfectly. But rest is not essential to coagulation: for the coagulated fibrine may be quickly obtained from blood by stirring it with a bundle of small twigs; and whenever any rough points of earthy matter or foreign bodies are introduced into the blood-vessels, the blood soon coagulates upon them. Neither is rest sufficient for the coagulation of the blood when other conditions are unfavourable; for coagulation is very slow in the body after death, although the blood is motionless.

Again, the *multiplication of points of contact* seems a favourable condition for coagulation. Thus, when all other conditions are unfavourable, the blood will coagulate upon rough bodies projecting into the vessels; as, for example, upon threads passed through arteries or aneurismal sacs, on the heart's valves roughened by inflammatory deposits or calcareous accumulations. And, perhaps, this may explain the quicker coagulation of blood after death in the heart with walls made irregular by the fleshy columns, than in the simple smooth-walled arteries and veins.

The *free access of air* is perhaps of all external conditions that which is most favourable to coagulation. It was formerly supposed to be so by reason of its favouring the exhalation of carbonic acid from the blood; for many experiments by Dr.

Polli (xc. April, 1843) seem to show, that, the more freely carbonic acid can be evolved, the quicker is the coagulation of the blood; and that the larger the quantity of the same gas contained in the blood, the slower is its coagulation. But latterly, Dr. B. W. Richardson has shown that the act of coagulation is intimately connected with the escape of ammonia from the blood (ccxxiv.). His researches show that if the evolution of ammonia be prevented, coagulation is retarded; and that a like retardation is effected by the introduction of even a very small quantity of this substance into the blood while yet liquid. Moreover, in further support of his opinion that ammonia is the solvent by which the fibrine is kept liquid in the circulating blood, he has shown that even after coagulation it may be re-dissolved in a solution of ammonia, and that re-coagulation will take place when the escape of ammonia is permitted.

Aided by Dr. Richardson's observations, we can now more readily comprehend the influence of many of the circumstances known to prevent, retard, or hasten, the act of coagulation, especially the many facts which shew that coagulation is accelerated by the free access of air, and retarded by the opposite condition. Thus, it is quick when blood is drawn slowly, and slow when it is drawn quickly; because, in the former case, the blood is more fully exposed to the atmosphere than in the latter, and the escape of ammonia proportionately favoured. To this also we may refer it, that coagulation is quicker in shallow, than in tall and narrow, vessels; because in the former a large surface of blood is exposed to the air; and to this (at least, in some measure) that the blood in the dead body often remains fluid for from twelve to twenty-four hours after death, and then coagulates within a few minutes after it is let out of the vessels and exposed to the air.

There is, however, something more than the mere escape of ammonia concerned in coagulation; and the observations of Professor Lister and others, clearly point to the withdrawal of the influence of living vessels as its principal cause (clxxxix. April, 1858; and 1859, p. 536. See also Brücke, l. c.)

It has been believed, and chiefly on the authority of Mr. Hunter, that, after certain modes of death, the blood does not coagulate: he enumerates the deaths by lightning, over-exertion (as in animals hunted to death), blows on the stomach, fits of anger. He says, "I have seen instances of them all." Doubtless, he had done so; but the results of such events are not constant. The blood has been often observed coagulated in the bodies of animals killed by lightning or an electric shock; and Mr. Gulliver (lxxi. vol. xli. p. 1087) has published instances in which he found clots in the hearts of hares and stags hunted to death, and cocks killed in fighting.

*The Blood-Corpuscles or Blood-Cells.*

It has been already said, that the clot of blood contains, with the fibrine and the portion of the serum that is soaked in it, the *blood-corpuscles*, or *blood-cells*. Of these there are two principal forms, the red and the white corpuscles, of which the latter, at least many of them, are in process of being developed into the former. When coagulation has taken place quickly, both kinds of corpuscles may be uniformly diffused through the clot; but, when it has been slow, the red corpuscles, being the heaviest constituent of the blood, tend by gravitation to accumulate at the bottom of the clot; and the white corpuscles, being among the lightest constituents, collect in the upper part, and contribute to the formation of the buffy coat.

The *human red blood-corpuscles* (pl. 1, fig. 1) are circular flattened cells of different sizes, the majority varying in diameter from $\frac{1}{3000}$ to $\frac{1}{4000}$ of an inch, and about $\frac{1}{10000}$ of an inch in thickness.* Their borders are rounded; their surfaces, in their most perfect and usual state, slightly concave; but they readily acquire flat or convex surfaces when, the liquor sanguinis being diluted, they are swollen by absorbing more fluid into their cavity. They are composed of a delicate and probably colourless, membranous cell-wall, which encloses a

* Mr. Gulliver has given, in his Edition of Hewson's works, p. 237, a table of the sizes of the red corpuscles in numerous species of vertebrate animals.

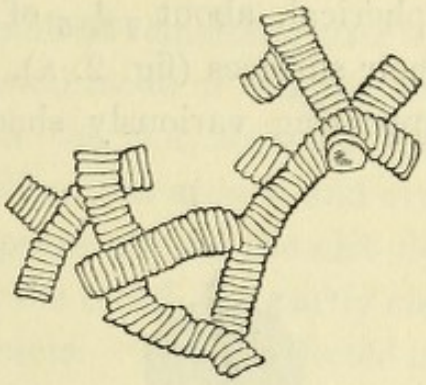
peculiar substance impregnated with the red colouring matter, or hæmatine. Their cell-walls are tough and elastic, so that, as they circulate, they admit of elongation and various changes of form in adaptation to the vessels, yet recover their natural shape as soon as they escape from compression. They have no nuclei, and their contents are probably homogeneous; at least they appear so, when their surfaces are flat or slightly convex; it is only when they are concave that the unequal refraction of transmitted light gives the appearance of a central spot, which is brighter or darker than the border according as it is viewed in or out of focus.

In examining a number of red corpuscles with the microscope, it is easy to observe certain natural diversities among them, though they be all taken from the same part. The great majority, indeed, are very uniform; but some are larger than these, and the larger ones generally appear paler and less exactly circular than the rest; their surfaces also are, usually, flat or slightly convex, they often contain a minute shining particle like a nucleolus, and they are lighter than the rest, floating higher in the fluid in which they are placed. These differences are connected with the development of the blood-corpuscles, and will be explained in the account of that process. Other deviations from the general characters assigned to the corpuscles, depend on changes that occur after they are taken from the body. Very commonly they assume a granulated form, in consequence, apparently, of a peculiar corrugation of their cell-walls. The larger cells are much less liable to this change than the smaller ones are, and the natural shape may be restored by diluting the fluid in which the corpuscles float; by such dilution the corpuscles, as already said, may be made to swell up by absorbing the fluid; and, if much water be added, they will become spherical and pellucid, their colouring matter being dissolved, and, as it were, washed out of them. Some of them may thus be burst; the others are made obscure; but many of these may be brought into view again by evaporating, or adding saline matter to, the fluid, so as to

restore it to its previous density. The changes thus produced by water are more quickly effected by weak acetic acid, which immediately makes the corpuscles pellucid, but dissolves few or none of them, for the addition of an alkali so as to neutralize the acid will restore their form, though not their colour.

A peculiar condition of the red corpuscles in inflammatory blood—a condition which appears to exist naturally in the blood of horses—is the principal cause of the formation of the buffy coat. It gives them a great tendency to adhere together in rolls or columns, like piles of coins, and then, very quickly, these rolls fasten together by their ends, and cluster; so that, when the blood is spread out thinly on a glass, they form a kind of irregular network, with crowds of corpuscles at the several points corresponding with the knots of the net (Fig. 1). Hence, the clot formed in such a thin layer of blood, looks mottled with blotches of pink upon a white ground: in a larger quantity of such blood, as soon as the corpuscles have clustered and collected in rolls (that is, generally in two or three minutes after the blood is drawn), they begin to sink very quickly; for in the aggregate they present less surface to the resistance of the liquor sanguinis than they would if sinking separately. Thus quickly sinking, they leave above them a layer of liquor sanguinis, and this coagulating forms a buffy coat, the volume of which is augmented by the white corpuscles, which have no tendency to adhere to the red ones, and by their lightness float up clear of them.

*Fig.* 1*.



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* (Fig. 1). Red corpuscles collected into rolls (after Henle); the appearance is also well represented by Mr. Wharton Jones (xciv. vol. lx. p. 311), who first very accurately described it. See also, for some interesting facts connected with it, Gulliver in his Edition of Hewson's Work.

The *white corpuscles* are much less numerous than the red ones. On an average, in health, there may be one white to fifty red corpuscles; but, in disease, the proportion is often as high as one to ten, and sometimes even much greater (clxxxix. *Jan.* 1851, p. 17, and lxxi. 1851, p. 147). They present greater diversities of form than the red ones do; but the gradations between the extreme forms are so regular, that no sufficient reason can be found for supposing there is, in healthy blood, more than one species of white corpuscles. In their most general appearance, they are circular and nearly spherical, about $\frac{1}{2500}$ of an inch in diameter, tuberculated on their surfaces (fig. 2. A). They have a greyish, pearly look, appearing variously shaded or nebulous, the shading being

*Fig.* 2*

much darker in some than in others. They seem to be formed of some white substance, variously refracting the light, and containing granules which are in some specimens few and very distinct, in others (though rarely) so numerous that the whole corpuscle looks like a mass of granules.

In a few instances, a distinct cell-membrane can be at once traced round a corpuscle thus composed; but, much more commonly, none can be demonstrated, till water or diluted acetic acid being added penetrates the corpuscle, and lifts up and distends a cell-wall, to the interior of which the material, that before appeared to form the whole corpuscle, remains attached as the nucleus of the cell. Thus these corpuscles are demonstrated to be nucleated cells, the nuclei of which are soft,

* Fig. 1. White corpuscles of the blood, highly magnified. A. A corpuscle in its natural condition. B and C. Different appearances produced by the action of diluted acetic acid.

granular, or tuberculated masses, and fill the cavities of the cells. The diversities presented by the nuclei which, by the action of water, are sometimes scarcely changed, sometimes broken into two or three pieces (fig. 1, c), and sometimes completely disintegrated and diffused through the cell, appear to be connected with the development of the corpuscles, and will be again referred to. So will the relation between the white and the red corpuscles.

### *The Serum.*

The *serum* is the liquid part of the blood remaining after the coagulation of the fibrine. In the usual mode of coagulation, part of the serum remains soaked in the clot, and the rest, squeezed from the clot by its contraction, lies around and over it. The quantity of serum that appears around the clot depends partly on the total quantity in the blood, but partly also on the degree to which the clot contracts. This is affected by many circumstances: generally, the faster the coagulation the less is the amount of contraction; and, therefore, when blood coagulates quickly, it will appear to contain a small proportion of serum. Hence, the serum always appears deficient in blood drawn slowly into a shallow vessel, abundant in inflammatory blood drawn into a tall vessel. In all cases, too, it should be remembered, that, since the contraction of the clot may continue for thirty-six or more hours, the quantity of serum in the blood cannot be even roughly estimated till this period has elapsed.

The serum is an alkaline, slimy or viscid, yellowish fluid, often presenting a slight greenish, or greyish hue, and with a specific gravity of from 1025 to 1030. It is composed of a mixture of various substances dissolved in about nine times their weight of water. It contains, indeed, the greater part of all the substances enumerated as existing in the blood, with the exceptions of the fibrine, globuline, and hæmatine. Its principal constituent is albumen, of which it contains about 8 per cent., and the coagulation of which, when heated, con-

verts nearly the whole of the serum into a solid mass. The liquid which remains uncoagulated, and which is often enclosed in little cavities in the coagulated serum, is called *serosity*: it contains, dissolved in water, fatty, extractive, and saline matters.

### *Chemical Composition of the Blood.*

Among the many analyses of the blood that have been published, some, in which all the constituents are enumerated, are inaccurate in their statements of the proportions of those constituents; others, admirably accurate in some particulars, are incomplete. The two following tables, constructed chiefly from the analyses of Denis, Lecanu, Simon, Nasse, Lehmann, Becquerel, Rodier, and Gavarret, are designed to combine, as far as possible, the advantage of accuracy in numbers with the convenience of presenting at one view a list of all the constituents of the blood.

Average proportions of the principal constituents of the blood in 1000 parts:—

| | |
|---|---|
| Water | 784· |
| Red corpuscles | 131· |
| Albumen of serum | 70· |
| Saline matters | 6·03 |
| Extractive, fatty, and other matters | 6·77 |
| Fibrine | 2·2 |
| | 1000· |

Average proportions of all the constituents of the blood in 1000 parts:—

| | | |
|---|---|---|
| Water | | 784· |
| Albumen | | 70· |
| Fibrine | | 2·2 |
| Red Corpuscles: | Globuline | 123·5 |
| | Hæmatine | 7·5 |

| | | | |
|---|---|---|---|
| Fatty Matters: | Cholestearine | 0·08 | 1·3 |
| | Cerebrine | 0·4 | |
| | Seroline | 0·02 | |
| | Oleic and margaric acids | | |
| | Volatile and odorous fatty acid | | |
| | Fat containing phosphorus | | |
| Inorganic Salts: | Chloride of sodium | | 3·6 |
| | Chloride of potassium | | 0·36 |
| | Tribasic phosphate of soda | | 0·2 |
| | Carbonate of soda | | 0·84 |
| | Sulphate of soda | | 0·28 |
| | Phosphates of lime and magnesia | | 0·25 |
| | Oxyde and phosphate of iron | | 0·5 |
| Extractive matters, biliary colouring matter, gases, and accidental substances | | | 5·47 |
| | | | 1000· |

Elementary composition of the dried blood of the ox:—

| | |
|---|---|
| Carbon | 57·9 per cent. |
| Hydrogen | 7·1 |
| Nitrogen | 17·4 |
| Oxygen | 19·2 |
| Ashes | 4·4 |

These results of the ultimate analysis of ox's blood afford a remarkable illustration of its general purpose, as supplying the materials for the renovation of all the tissues. For the same analysts (Playfair and Boeckmann) have found that the flesh of the ox yields the same elements in so nearly the same proportions, that the elementary composition of the organic constituents of the blood and flesh may be considered identical, and may be represented for both by the formula $C_{45}H_{39}N_6O_{15}$.

After what has been said of many of the constituents of the blood, in the chapter on the CHEMICAL COMPOSITION OF THE BODY, a few words on each of the principal of them may here suffice.

The *water of the blood* is subject to hourly variations in its quantity, according to the period since the taking of food, the amount of bodily exercise, the state of the atmosphere, and all

the other events that may affect either the ingestion or the excretion of fluids. According to these conditions, it may vary from 700 to 790 parts in the thousand. Yet uniformity is on the whole maintained; because nearly all those things which tend to lower the proportion of water in the blood, such as active exercise, or the addition of saline and other solid matter, excite thirst; while, on the other hand, the addition of an excess of water to the blood is quickly followed by its more copious excretion in sweat and urine. And these means for adjusting the proportion of the water find their purpose in maintaining certain important physical conditions in the blood; such as its proper viscidity, and the degree of its adhesion to the vessels through which it ought to flow with the least possible resistance from friction. On this also depends, in great measure, the activity of absorption by the blood-vessels, into which no fluids will quickly penetrate, but such as are of less density than the blood. Again, the quantity of water in the blood determines, chiefly, its volume, and thereby the fulness and tension of the vessels, and the quantity of fluid that will exude from them to keep the tissues moist. Finally, the water is the general solvent of all the other materials of the liquor sanguinis, and its abundance greatly favours organic chemical action: for generally, and within limits of health, the amount of action in the organic life of the several parts of the body is in direct proportion to the quantity of water they severally contain. Compare, *e.g.*, in these respects, the bones or tendons with the muscles; or any tissue with the blood; or any of the tissues of young animals with the same in old ones: in all such cases, abundant water appears connected with activity of organic life.

It is remarkable, that the proportion of water in the blood may be sometimes increased even during its abstraction from an artery or vein. Thus Dr. Zimmerman (ix. vol. iv. p. 385), in bleeding dogs, found the last drawn portion of blood contain 12 or 13 parts more of water in 1000 than the blood first drawn; and Polli (xci.) noticed a corresponding diminution in

the specific gravity of the human blood during venesection, and suggested the only probable explanation of the fact, namely, that during bleeding, the blood-vessels absorb very quickly a part of the serous fluid with which all the tissues are moistened.

The *albumen* may vary, consistently with health, from 60 to 70 parts in the 1000 of blood. The form in which it exists in the blood is not yet certain. It may be that of simple solution as pure albumen: but it is, more probably, in combination with soda, as an albuminate of soda; for, if serum be much diluted with water, and then neutralized with acetic acid, pure albumen is deposited. Another view, entertained by Enderlin, (x. March and April, 1844), is that the albumen is dissolved in the solution of the tribasic phosphate of soda, to which he considers the alkaline reaction of the blood to be due, and solutions of which can dissolve large quantities of albumen and phosphate of lime.

The proportion of *fibrine* in healthy blood may vary between 2 and 3 parts in 1000. In some diseases, such as typhus, and others of low type, it may be as little as 1·034 ; in other diseases, it is said, it may be increased to as much as 7·528 parts in 1000. But, in estimating the quantity of fibrine, chemists have not taken account of the white corpuscles of the blood. These cannot, by any mode of analysis yet invented, be separated from the fibrine of mammalian blood: their composition is unknown, but their weight is always included in the estimate of the fibrine. In health, they may, perhaps, add too little to its weight to merit consideration: but in many diseases, especially in inflammatory and other blood-diseases in which the fibrine is said to be increased, these corpuscles become so numerous that a large proportion of the supposed increase of the fibrine must be due to their being weighed with it. On this account all the statements respecting the increase of fibrine in certain diseases need revision. The quantity of fibrine appears to be, generally rather greater in arterial than in venous blood; and to be less in the blood of

the splenic and portal veins than in ordinary venous blood. According to Denis, the fibrine of venous blood differs from that of arterial in that, when it is fresh and has not been much exposed to the air, it may be dissolved in a slightly heated solution of nitrate of potash.

*Globuline*, and *Hæmatine* or *Hæmatosine*, mixed in a compound which has been named *Hæmato-globuline* or *Cruor*, constitute the substance contained in the red blood-corpuscles. The cell-walls of these minute bodies cannot, indeed, be completely separated from their contents, or chemically distinguished from the globuline: and hence, perhaps, the diversity in the statements respecting the proportions of globuline and hæmatine. Berzelius states the proportion of hæmatine at 5·8 per cent. of the compound; Schmidt (x. No. lxi. p. 165) at 12·41 per cent. having, perhaps, more completely separated the walls from the contents of the blood-corpuscles.

*Globuline* appears to be a proteine-compound. According to Simon (lxxxii. vol. i. p. 81) it bears most resemblance to caseine, on which account he named it caseine of blood; but Liebig and others regard it as more similar to albumen. It is soluble in water, and its solution, when heated, forms a granular coagulum. Its chemical composition cannot be exactly determined, because it cannot be obtained quite pure from either hæmatine or the membranous walls of the blood-cells, the mixture of which, as Henle suggests (xxxvii. p. 55), is probably sufficient to explain its apparent differences from common albumen. It contains about 2 per cent. of sulphur.

*Hæmatosine* or *Hæmatine*, is distinguished from all other animal matter by its peculiar blood-colour, and by the changes which this colour presents when, being incorporated in the blood-corpuscles, it is exposed to oxygen, carbonic acid, and other gases. It is soluble in water, by which, as already said, it may, with the globuline, be washed out of the blood-corpuscles: and from this solution it is precipitated by most metallic salts, and by concentrated acids. In the living, or recent, state of the blood-corpuscles the hæmatine is confined within their

cell-walls, and appears to be insoluble in the serum; but when the blood begins to decompose, and the cell-walls, losing their texture, permit the outward passage of their contents, both the hæmatine and the globuline are dissolved in the serum, which thus becomes blood-coloured, and may impart its tinge to the surrounding parts. With the globuline, also, hæmatine, appears to be coagulated by heat; but, according to Mulder, it is only enclosed in the coagulum of the globuline, without being itself coagulable. In the purest state in which it can be obtained,* it is so far changed as to be insoluble in water, of a deep blackish brown colour, and not liable to change of colour on exposure to gases. Boiling alcohol will dissolve small quantities of it, and it is freely soluble in alcohol acidulated with sulphuric, hydrochloric, or nitric acid, and in weak solutions of potash, soda, or ammonia. According to Mulder, pure hæmatine consists of carbon, 65·84 per cent.; hydrogen, 5·37; nitrogen, 10·4; oxygen, 11·75; iron, 6·64. The presence of so large a proportion of iron constitutes a peculiar feature in hæmatine. The mode in which the metal exists in it has been much discussed. By some it is supposed to be in the form of an oxyde, or a salt, or in the form of peroxyde in arterial blood, and carbonate of the protoxyde of iron in venous blood (Liebig, xi.) But the greater probability is, that the iron is combined as an element with the four essential elements, carbon, hydrogen, nitrogen, and oxygen, in the same manner as, it is held, sulphur is combined with them in albumen, fibrine, cystic oxyde, etc. The principal evidence for this view, which is especially supported by Scherer and Mulder, is, 1, that when chlorine, which would not decompose an oxyde of iron, is passed through a solution of hæmatine, chloride of iron is formed, and the iron thus removed from the other elements of the hæmatine, is replaced by chlorous

* On the several modes of obtaining it, see Simon (lxxxii), Fownes (lx.), Griffiths (cii.), and Garrod (xxx. 1848, vol. i. p. 654): consult also Lehmann (ccxxii. p. 137).

acid; 2, that all the iron may be removed from hæmatine by sulphuric acid, without abstracting from it any of its oxygen, which would not be possible if the iron were more intimately united with the oxygen than with the other elements of the hæmatine; 3, that pure hæmatine may be exposed for several days to the action of dilute hydrochloric or sulphuric acid, without any loss of its iron; though these acids would dissolve an oxyde of iron or decompose a carbonate.

The peculiar colour of hæmatine depends less on the iron than on its other constituents, for, as Scherer and Mulder have shewn, hæmatine may retain its colour after all the iron is extracted from it. Therefore the changes of colour produced by respiration, and the contact of gases with the blood, cannot be referred to any change in the state of the iron in the hæmatine. It is, indeed, very doubtful whether the rapid change of colour which is effected in respiration, and on the contact of various gases, can be referred to any chemical changes whatever in the hæmatine; much more probably, it is due to changes in the form of the blood-corpuscles and their consequently different modes of reflecting and transmitting light. For, 1, the changes of colour produced by carbonic acid and oxygen mixed with a solution of the colouring matter of the blood are very slight; they are generally scarcely perceptible, and when they are seen they are slowly produced, or are not more than may be explained by the action of the gases on some corpuscles still suspended in the solution; 2, the same changes of colour as are produced by carbonic acid and oxygen acting on the corpuscles, may be produced by distilled water, and strong solutions of alkaline salts. A black clot of blood becomes at once scarlet by washing it with salt, and is not blackened again by carbonic acid; a scarlet one is made black by washing it with distilled water, and is only very slowly reddened again by the contact of oxygen. Now the changes thus produced by salt and by water acting on the corpuscles, are not produced by the addition of the same substances to a solution of hæmatine, and are

not connected with any chemical change in that substance or in the corpuscles: but they are connected with alterations in the shape of the red corpuscles; for saline solutions, if denser than the liquor sanguinis, contract and shrivel up the corpuscles, making them deeply bi-concave; and distilled water has the contrary effect, swelling out the corpuscles, and making them thickly bi-convex or spherical. Changes corresponding with these are produced by the contact of oxygen and of carbonic acid with the corpuscles: the former contracting them, and making their cell-membranes thick and granular; the latter dilating them, and thinning, and finally dissolving their cell-walls; and effecting these changes in a degree which, however slight it may appear in a single corpuscle, is enough to account for the change of colour in a mass of blood. Herein, then, is a sufficient explanation of the changes that the corpuscles undergo, without supposing any immediate chemical alteration in the hæmatine; an alteration which should take place as well in a solution of hæmatine as in the corpuscles.

The opinion, that the instantaneous change of colour which takes place in blood exposed to the action of oxygen or carbonic acid is due to a physical rather than a chemical alteration in the corpuscles, is quite consistent with the probability that the corpuscles are chemically changed by the longer action of those gases dissolved in the blood. It appears that entire blood will absorb much more oxygen than either serum or liquor sanguinis alone will; as if it were chiefly with the corpuscles that the absorbed oxygen combines. If this be true, we may conclude, from the whole, that the oxygen, by first contracting the corpuscles and thickening their walls, makes them so reflect light, as to appear, in mass, bright-red, and then chemically combines with them; and that carbonic acid, by dilating them and thinning their walls, makes them reflect less light, and appear, in mass, nearly black; but we have no means of determining how large a portion of the oxygen inspired combines with the

corpuscles, nor whether that portion combines with the hæmatine or the globuline, or equally with both.*

The enumeration of the *fatty matters* of the blood makes it probable that most of those which are found in the tissues or secretions exist also ready-formed in the blood; for it contains the cholestearine of the bile, the cerebrine and phosphorised fat of the brain, and the margaric and oleic acids of common fat. The fat named seroline appears to be peculiar to the blood. The volatile fatty acid is that on which the odour of the blood mainly depends; and it is supposed, that when the sulphuric acid is added (see p. 36), it evolves the odour by combining with the base with which, naturally, this fat is neutralised.

The fatty matters of the blood are subject to much variation in quantity, being commonly increased after every meal in which fat, or starch, or saccharine substances have been taken. At such times, the fatty particles of the chyle, added quickly to the blood, are only gradually assimilated; and their quantity may be sufficient to make the serum of the blood opaque, or even milk-like.

Of the *inorganic constituents* of the blood,—the substances which remain as *ashes* after its complete burning—one may observe in general their small quantity in proportion to that of animal matter contained in it. Those among them of peculiar interest are the phosphate and carbonate of soda, and the phosphate of lime. It appears most probable, that the blood owes its alkaline reaction to both these salts of soda. The existence of the tribasic phosphate, a salt consisting of one equivalent of phosphoric acid with two of soda and one of basic water ($PO_5 + 2N_a O + HO$) was proved by Enderlin

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* The treatises on this subject are discussed by Scherer, in his several reports in Canstatt's Jahresberichte since 1844. The chief original works are those of Scherer, Bruch, and Reuter, in Henle and Pfeufer's Zeitschrift from 1843 to 1847; Donders, Harless, Marchand, and Mulder.

(x. 1844): the presence of carbonate of soda has been proved by Lehmann and others.

In illustration of the characters which the blood may derive from the phosphate of soda, Liebig points out the large capacity which solutions of that salt have of absorbing carbonic acid gas, and then very readily giving it off again when agitated in atmospheric air, and when the atmospheric pressure is diminished. It is probably, also, by means of this salt, that the phosphate of lime is held in solution in the blood in a form in which it is not soluble in water, or in a solution of albumen.* Of the remaining inorganic constituents of the blood,—the oxyde and phosphate of iron referred to exist in the liquor sanguinis, independent of the iron in the corpuscles.

Among the *extractive matters* of the blood, the most noteworthy are *Kreatine* and *Kreatinine*. Besides these, other organic principles have been found either constantly or generally in the blood, including *caseine*, especially in women during lactation: *glucose*, or *grape-sugar*, found in great abundance in the blood of the hepatic vein, but disappearing largely during its transit through the lungs (Bernard); *urea*, and, in very minute quantities, *uric acid* (Garrod): *hippuric* and *lactic acids*: *ammonia* (Richardson): and lastly, certain *colouring* and *odoriferous* matters. The various GASES found in the blood, will be spoken of in the Chapter on RESPIRATION.

When blood has been at rest for some time, either within or without the body, and especially if diluted with water, crystals of various kinds not unfrequently form in it. They are very

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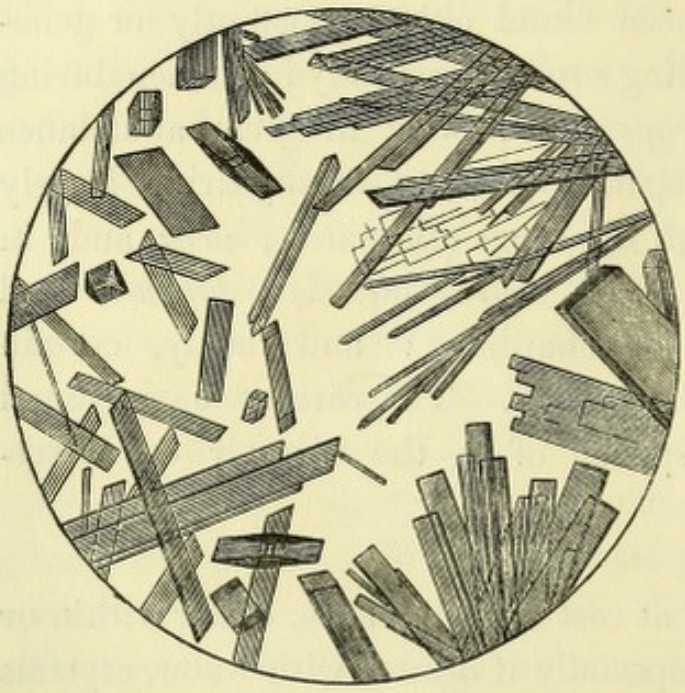
* The student will do well to refer to the interesting observations of Liebig, in his Chemistry of Food, respecting the mode in which the phosphate of soda is formed for the blood of herbivorous animals who take, in their food, phosphate of potash and chloride of sodium: and respecting the mutual action of the alkaline phosphate in the blood and the acid phosphate in the juice of the muscles.

common in the coagula within aneurismal sacs, in apoplectic clots, and in other masses of extravasated blood. Such crystals may also often be formed artificially, by exposing a drop of recently drawn blood, diluted with water, to the air for a few minutes, and then breathing upon it. The carbonic acid of the breath seems to be influential in their production. Indeed, Lehmann is of opinion that both carbonic acid and oxygen are essential to their formation, and that they act by inducing a chemical change in the contents of the blood-cells (ccxxi. p. 136.) In some cases, however, the blood crystallizes at once, on simple exposure to the air: in others, more complex processes have to be resorted to for the production of crystals. Whether formed naturally or artificially, the blood crystals, (figs. 3, 4, and 5) have nearly always a more or less red colour, vary much in size and shape, not only in the blood of different animals, but in the same blood at different stages of its decomposition, and also present diversities in chemical composition, some being soluble in one re-agent, some in another. The substance of which they are composed, has been especially studied by Lehmann; it appears to be of an albuminous nature, and probably results from a retrograde transformation of the component parts of the red

*Fig.* 3*.



* Figs. 3, 4, and 5 illustrate some of the principal forms of blood-crystals:—

Fig. 3, Prismatic, from human blood.

Fig. 4, Tetrahedral, from blood of the guinea-pig.

corpuscles, namely, the *hæmato-globuline.*

For the best account of this interesting subject, which is still involved in much obscurity, the student is referred to Lehmann (cciii. vol. iii., pp. 485—495, ccxxi. p. 133); to a good review of it by Dr. Sieveking (cxc. vol. xii., p. 348); to Dr. Day's Report on Animal Chemistry (cxc. vol. xv., p. 547.); and to the various reports in Canstatt's Jahresbericht.

*Fig.* 4.

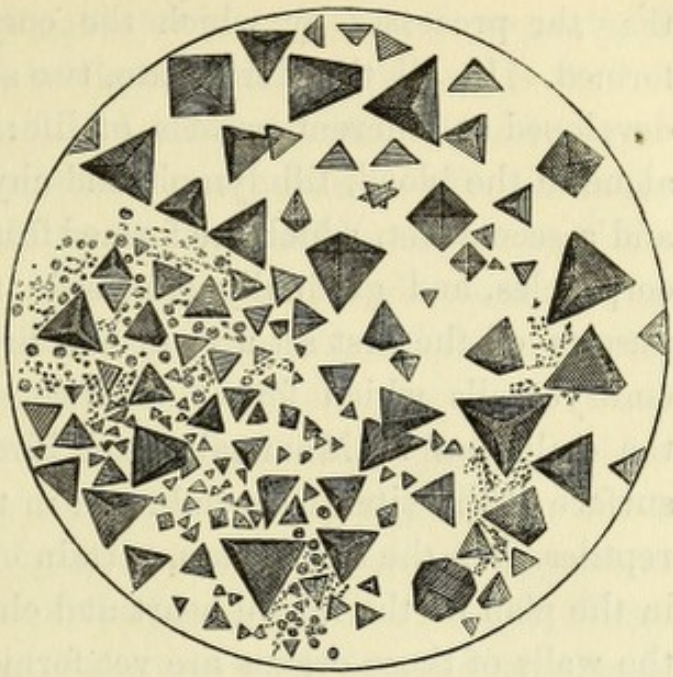
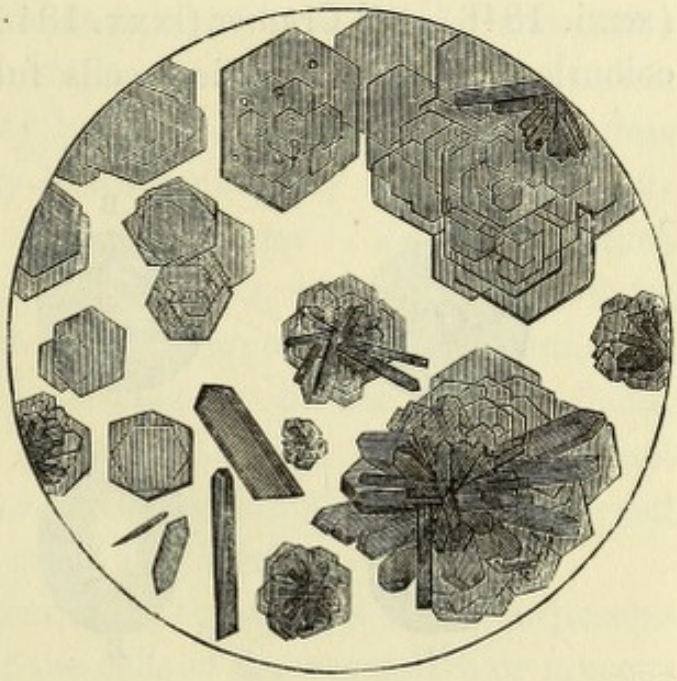


*Fig.* 5.



### *Vital Properties and Actions of the Blood.**

The life of the blood is chiefly manifested in its development and self-maintenance, in its liability to idiopathic disease and death, and in the purpose and relation which connect it with the other living parts.

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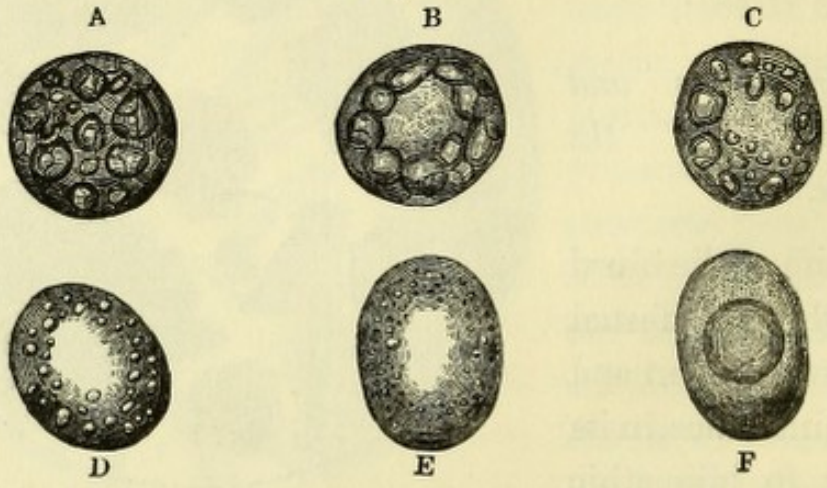
Fig. 5, Hexagonal crystals, from blood of squirrel. On these six sided plates, prismatic crystals, grouped in a stellate manner, not unfrequently occur; (after Funke, cciv.)

* The following portion of this chapter contains an abstract of part of the Lectures on the Life of the Blood, delivered by Mr. Paget, at the College of Surgeons, in May, 1848.

In the *development* of the blood, little more can be traced than the processes by which the corpuscles and fibrine are formed. In all the Vertebrata, two sets of red corpuscles are developed at different periods of life: a first set, which exist alone in the blood, till lymph and chyle begin to be formed; and a second set, which are formed from the lymph- and chyle-corpuscles, and gradually supersede the first set. The corpuscles of the first set are, in the first instance, part of the embryo-cells which form the mucous or vegetative layer of the embryoes in Mammalia and birds, and the whole inner surface of the vitelline membrane, in the embryoes of fish and reptiles. In the latter class, certain of these cells are laid out in the plan of the future heart and chief blood-vessels, before the walls of those organs are yet formed, and before the blood has begun to move. As described by Vogt (cv.), Kölliker (xxxi. 1846), and Cramer (lxxx. 1848, p. 631), they are large colourless vesicular spherical cells full of yellowish particles

*Fig.* 6.*




of a substance like fatty matter (fig. 6, A); many of which particles are quadrangular and flattened, and have been called

* Fig. 6. Development of the first set of blood-corpuscles in the Batrachian larva. A. An embryo-cell filled with fatty-looking particles. B, C, D, and E. Successive stages in the transition of the embryo-cell to a blood-corpuscle, as described in the text. F. A fully-formed blood-corpuscle.

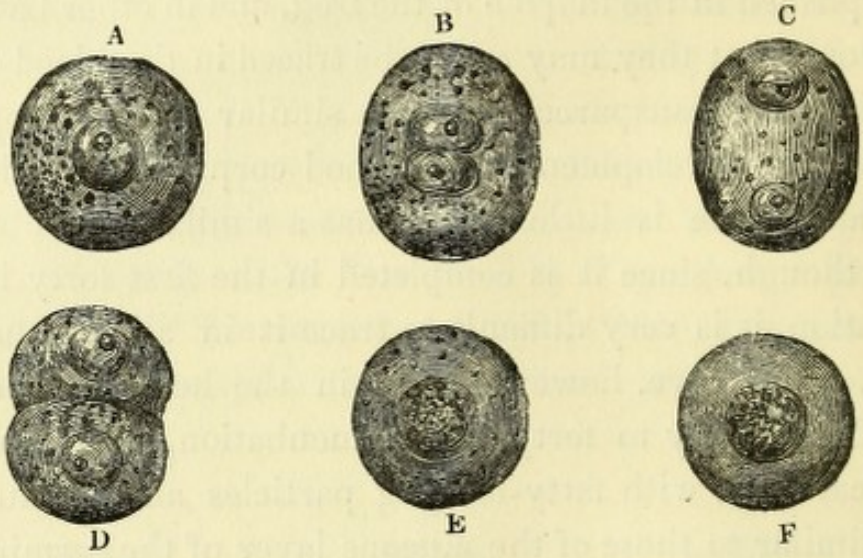
stearine-plates, though they are not proved to consist of that or any other unmixed fatty substance. Among these particles each cell has a central nucleus, which, however, is at first much obscured by them. The development of these embryo-cells into the complete form of the corpuscles is effected by the gradual clearing up, as if by division and liquefaction, of the contained particles, the acquirement of blood-colour, and of the elliptical form, the flattening of the cell, and the more prominent appearance of the nucleus. The changes are so slowly accomplished in the tadpole of the frog, and in other batrachian embryoes, that they may easily be traced in the blood while it flows in their transparent parts; a similar process appears to occur in the development of the blood-corpuscles of fish (Vogt, civ.), and there is little doubt that a similar one obtains in birds, though, since it is completed in the first forty hours of incubation, it is very difficult to trace it in all its successive stages. We have, however, seen in the heart of the chick, after from thirty to forty hours' incubation, some colourless spherical cells, with fatty-looking particles and granules, exactly similar to those of the mucous layer of the germinal area of the ovum. With these were others, which appeared to be of the same origin, but to have undergone changes similar to those above-described: a clearing up of the fatty particles, acquirement of colour, reduction of size, and more distinct appearance of the nucleus. The assumption of the flattened elliptical form occurs in birds at a later period.

In mammalian embryoes, also, the earliest blood-corpuscles appear to be a portion of the cells of the vegetative or mucous layer of the germinal area. They are large, spherical or oval, pellucid and colourless, nucleated, and full of minute granules, (fig. 7, A). In these we have observed (as Kölliker, xxxiii. 1846, Fahrner, cvi., and others have done), a process of multiplication by bi-partition of the nucleus, each half of which, either by appropriating half the cell, or by developing a cell around itself, becomes the central nucleus of a new cell differing from the parent-cell from which it escapes, in little except

in being smaller and more generally circular (B, C, and D). The subsequent changes of these cells resemble those already described; they gradually acquire the blood-colour, their granules disappear, and their surfaces become smoother and more uniform (E and F).

It seems, moreover, that in the mammalian corpuscles, these changes may ensue as well during, as after, the multiplication

*Fig. 7.**




by partition of the nucleus: for red corpuscles are not unfrequent in mammalian embryoes containing two nuclei, and we have seen some with three, and even four, nuclei.

The development of the first set of blood-corpuscles appears, thus, to be uniform in all the classes of Vertebrata; namely, in all, from the embryo-cells of the vitelline membrane or germinal area, into nucleated red blood-cells; the principal visible changes being the disappearance of granules or fatty-looking substance, the greater prominence of the nucleus, and

* Fig. 7. Development of the first set of blood-corpuscles in the mammalian embryo. A. A dotted, nucleated embryo-cell in process of conversion into a blood-corpuscle: the nucleus provided with a nucleolus. B. A similar cell with a dividing nucleus; at C, the division of the nucleus is complete; at D, the cell also is dividing. E. A blood-corpuscle almost complete, but still containing a few granules. F. Perfect blood-corpuscle.

the acquirement of colour. And, in their most perfect state, the corpuscles of the first set are, in all the vertebrate classes, nucleated cells. Those of the human embryo are circular, thickly disk-shaped, full-coloured, and, on an average, about $\frac{1}{2500}$th of an inch in diameter: their nuclei which are about $\frac{1}{5000}$th of an inch in diameter, are central, circular, very little prominent on the surfaces of the cell, and apparently slightly granular or tuberculated. In a few instances, cells are found with two nuclei; and such cells are usually large and elliptical, with one of the nuclei near each end of their long axis.

When, in the development of the embryo, the lymph and chyle begin to be formed and added to the blood, their corpuscles are developed so as to supersede those produced in the manner just described. In some species (as in the frog) the first appearance of lymph- and chyle-corpuscles in the blood exactly corresponds with the time at which the external branchiæ disappear; in others, as in the chick, rabbit, ferret, and sheep, their appearance coincides with the closure of the branchial fissures.* After they have once appeared, the new blood-corpuscles appear to be derived exclusively through them. For some time, indeed, the two sets of corpuscles appear mingled in the blood. In this case, in Mammalia, the white corpuscles of the first set (if any remain in this stage) are distinguished from those of the second set, by their larger size, distinct cell-walls, small well-defined central nuclei, and their pellucid contents with very minute scattered dots or granules; and the red corpuscles of the first set are always characterised by their larger size and their nuclei, which, if not at once distinct, are rendered so by the addition of water. But, gradually, while the corpuscles of the

* These instances prove a frequent coincidence in the development of the blood by the production of a new set of corpuscles through lymph and chyle, and of the respiratory apparatus by the suppression of the external branchial organs. But, in the Triton punctatus, we have found lymph-corpuscles in the blood while its long-retained external branchiæ still exist.

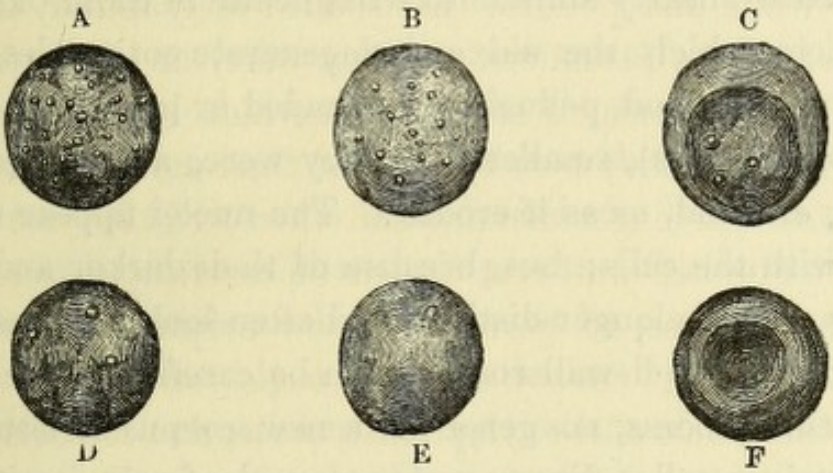
second set are increasing, those of the first disappear, and we believe they would not be found in a human embryo of more than two months old, unless in cases of arrested development; in such an one, where the abdominal walls were incomplete, we found the two sets of corpuscles mixed in the blood of a fœtus between three and four months old.

The origin and first formation of the lymph and chyle and of their corpuscles will be described in the chapter on ABSORPTION; the structure of the corpuscles (which are the white or colourless corpuscles of most writers, the granule-cells of Mr. Wharton Jones) is described already (p. 48). In the different vertebrate classes, there is much greater similarity in these corpuscles than in the red blood-corpuscles of the second set. Except for some difference of size, the same general description might apply to all; and some features in the development are alike in all, namely, the gradual clearing up, as if by deliquescence, of their granular contents, and a commensurate acquirement of colour. But, while in the corpuscles of the oviparous Vertebrata the outer part alone of their granular contents thus clears up, and the central part remains as the small nucleus of the complete blood-cell, in man, and all Mammalia, the whole of the contents clear up, acquire a uniform colour, and become the homogeneous contents of a cell without a nucleus.

The principal steps in the development of the human lymph- or chyle-corpuscle into the red-corpuscle, may be traced in specimens of blood in which these white corpuscles are numerous. The white corpuscle, at first tuberculated, containing many granules, and darkly-shaded (fig. 8, A), becomes smoother, paler, less granular, and more dimly shaded or nebulous (fig. 8, B): changes corresponding with those which Mr. Wharton Jones describes as from the coarsely to the finely granular stage of the *granule-cell* (xliii. 1846). In these stages, the cell-wall may be easily raised from its contents by the contact and penetration of acetic acid, or by the longer action of water (fig. 8, C); and, according to the stage of development, so, as already stated, are the various appearances which the contents of the cell thus acted on present. In the regular progress of development, it

becomes at length impossible to raise the cell-wall from its contents. Then the corpuscles acquire a pale tinge of blood-colour; and this always coincides with the softening of the shadows which before made them look nebulous, and with the final vanishing of all the granules, with the exception sometimes of one which remains some time longer like a shining particle in the corpuscle, and has probably been often mistaken for a

*Fig.* 8.*




nucleus (fig. 8, E). The blood-colour now deepens; and at the same rate the corpuscles become smooth and uniform; bi-concave, having previously gradually changed the nearly spherical form for a lenticular or flattened one; smaller, apparently by condensation of their substance, for at the same time they become less amenable to the influence of water; more liable to corrugation and to collect in clusters; and heavier, so that the smallest and fullest-coloured corpuscles always lie deepest in the field. Thus the most developed state of the mammalian red corpuscle appears to be that in which it is full-coloured, circular, bi-concave, small, uniform, and heavy: this also is the

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* Fig. 8. Development of human lymph- and chyle-corpuscles into blood-corpuscles. A. A lymph- or white blood-corpuscle. B. The same in process of conversion into a red-corpuscle. C. A lymph-corpuscle with the cell-wall raised up round it by the action of water. D. A lymph-corpuscle from which the granules have almost all disappeared. E. A lymph-corpuscle acquiring colour; a single granule, like a nucleus, remains. F. A red corpuscle fully developed.

state in which the corpuscles appear to live the longer and more active portion of their lives.

This mode of development of new blood-corpuscles from those of the lymph and chyle, continues throughout life. New corpuscles never appear to be produced from the germs of old ones; when a corpuscle is past its perfection, it degenerates, and probably liquefies. The changes of such degeneration have not been clearly seen in mammalian corpuscles; but they are probably nearly similar to what occur in those of fish and reptiles, in which the old and degenerate corpuscles appear perfectly white and pellucid (not shaded or granular, like the lymph-corpuscles), smaller than they were, and, in some instances, cracked, or as if eroded. The nuclei appear to degenerate with the cells; but, because of their darker and harder outlines, remain longer distinct, and often look like free nuclei, unless the dim cell-wall round them be carefully searched for. But in this process, no germ for a new corpuscle issues from the transient cell. Every new corpuscle forms itself in and from the materials of the lymph and chyle, and is perfected in the blood; and the blood is maintained by constant repetitions of this process. Herein, also, is provision for the welfare of the body: for, if the blood-corpuscles were, like many cells, derived from germs formed in their predecessors, then every loss of blood would involve the loss, not only of the corpuscles escaping at the time, but of all those that, in after time, should have descended from the lost ones and their germs. But new blood being made from lymph and chyle, its losses to any amount can be repaired, provided the processes for the formation of those fluids are not disturbed.

The development of fibrine appears to proceed commensurately with that of the second set of corpuscles. In the earliest state of the chyle, no fibrine exists; but when chyle-corpuscles are formed, the fluid in which they float is spontaneously coagulable; and the fibrine, whose existence is thus proved, appears to increase as the chyle proceeds onwards to the blood, and passes through the lacteal glands. Yet, in the

most perfect chyle and lymph the fibrine is less abundant, and coagulates less firmly than in the blood: we may therefore assume that its development, like that of the corpuscles, is perfected in the blood itself.

From what has been said, it will have appeared that when the blood is once formed, its *growth* and *maintenance* are effected by the constant repetition of the development of new portions. In the same proportion as the blood yields its materials for the maintenance and repair of the several solid tissues, and for secretions, so are new materials supplied to it in the lymph and chyle, and, by development, made like it. The part of the process which relates to the formation of new corpuscles and fibrine has been described; but it is probably only a small portion of the whole process; for the assimilation of the new materials to the blood must be perfect, in regard to all those immeasurably minute particulars by which the blood is adapted for the nutrition of every tissue, and the maintenance of every peculiarity of each. How precise the assimilation must be for such an adaptation, may be conceived from some of the cases in which the blood is altered by disease, and, by assimilation, is maintained in its altered state. For example, by the insertion of vaccine matter, the blood is for a short time manifestly diseased; however minute the portion of virus, it affects and alters, in some way, the whole of the blood. And the alteration thus produced, inconceivably slight as it must be, is long maintained; for, even very long after a successful vaccination, a second insertion of the virus may have no effect, the blood being no longer amenable to its influence, because the new blood, formed after the vaccination, is made like to the blood as altered by the vaccine virus; in other words, the blood exactly assimilates to its altered self the materials derived from the lymph and chyle. So, in all probability, are maintained the morbid states of the blood which exist in syphilis, and many other chronic diseases: the blood, once inoculated, retaining, by the exactness of its assimilation, the taint which it received, though, after a time, it may not have in it one of the

particles on which the taint first passed. In health we cannot see the precision of the adjustment of the blood to the tissues; but we may imagine it from the small influences by which, as in vaccination, it is disturbed, and we may be sure that the new blood is as perfectly assimilated to the healthy standard as, in disease, it is assimilated to the most minutely altered standard.*

The assimilation of the blood is probably effected, essentially and finally, by the formative power (see p. 28) which the blood possesses in common with the solid tissues. But it is ministered to and assisted by the actions of other parts; as, 1st, the digestive and absorbent systems, with probably the liver, and most or all of the vascular glands, whose especial office is to prepare materials, not only enough, but exactly fit to form the new blood; and, 2ndly, the excretory organs, through which the blood separates from itself materials which are refuse, such as the waste substance of the tissues, the urea, carbonic acid, etc., or are unfit to form part of its essential constituents, such as some of the materials taken for food and drink, and absorbed by the blood-vessels of the digestive canal without being formed into chyle. But, 3rdly, the precise constitution of the blood is adjusted by the balance of the nutritive processes for maintaining the several tissues, so that none of the materials appropriate for the maintenance of any part may remain in excess in the blood. Each part, by taking from the blood the materials it requires for its maintenance is, as Treviranus observed, (lxviii. bd. i. p. 401) in the relation of an excretory organ to all the rest. For example, if the muscles did not take materials for their nutrition, there might be an excess of fibrine and their other constituents in the blood; if the bones did not do so, the salts of lime would be in excess, and so on.†

The formative power by which the blood maintains itself is,

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* Corresponding facts in relation to the maintenance of the tissues by assimilation will be mentioned in the chapter on NUTRITION.

† See further on this subject ccix. p. 24 and succeeding Lectures.

perhaps, inherent in its whole substance. No sufficient reason appears for considering that it belongs to the corpuscles more than to any of the other highly organic constituents of the blood; neither is there any evidence for determining the particular functions of the corpuscles; only, it is probable that they help in the formation of materials appropriate for the nutrition of the tissues by acting like gland-cells, that is, by forming or elaborating in their cavities materials which they may discharge when perfect (see SECRETION). Both white and red corpuscles may do this, but the red ones more perfectly than the white; since, as a general rule, rudimentary parts have the same function as the perfect parts into which they are developed, but discharge that function with less power.

The *purpose* of the blood, thus developed and maintained, appears, in the perfect state, to be threefold: namely, 1st, to provide materials appropriate for the nutrition and maintenance of all the parts of the body; 2nd, to convey to the several parts oxygen, whether for the discharge of their functions, or for combination with their refuse matters; 3rd, to bring from the same parts those refuse matters, and convey them to where they may be discharged. The first is the principal and essential purpose of the blood; the second and third are subordinate purposes, which the blood discharges, as it were, by the way, and which will be considered in future chapters.

Of the first purpose little more is known, than that the blood does provide the materials for the maintenance of the body; and that they are not all in the blood in the same chemical compounds as they form in the tissues. Gelatine, for example, which forms so large a part of the tissues, does not exist in healthy blood, and must therefore be formed from some of its albuminous or proteine compounds while the tissues in which it is found are being developed.

It may be observed that the changes which materials taken from the blood and forming tissues undergo, though always processes of development in regard to structure, are sometimes degenerations in a chemical sense. The case of the gelatinous

tissues is an example of this; however highly organized their structure, their chemical composition is lower than that of the blood, gelatine being, as Dr. Prout has shewn (xxi. p. 455), the least remote from inorganic matter of any of the nitrogenous animal compounds. Thus, the providing of materials for the gelatinous tissues may be regarded as the lowest part of this office of the blood; the highest is, probably, the provision for the nervous and animal muscular systems. To these, and especially to the brain, the development of the blood appears to be peculiarly adjusted. Thus, in the Invertebrata that have blood, the observations of Mr. Wharton Jones (xliii. 1846) shew that the blood-corpuscles are not developed beyond the stage which the lymph-corpuscles commonly attain in the oviparous Vertebrata, though, up to that stage and in it, they are very similar to the lymph-corpuscles. Among the Vertebrata, the Branchiostoma, as a connecting link between the two classes, appears to have the same form of blood-corpuscles as the Invertebrata; but in other fish we find, coincidently with the great advance in the development of a brain and spinal cord, the introduction of a proportionally larger quantity of blood, and of red corpuscles formed by a further development of such corpuscles as are the most perfect in the Invertebrata. In the transition from fish to reptiles, the greater development of the brain is associated with a general further increase in the quantity and velocity of the blood; and in that from reptiles to birds with a yet much larger increase in its quantity and velocity, an augmentation of the proportion of fibrine, and a great multiplication of blood-corpuscles with reduction of their size. Lastly, with the greater development of the brain in Mammalia, we find the development of the blood-corpuscles into a higher form than they have in any other Vertebrata; for, though the nucleated cell is commonly regarded as a higher development than the cell without a nucleus, yet since, in the blood of the mammalian embryo, the latter supersedes the former, and is adapted to the general advance of development, we may be sure that, in this instance at least, the cell without a nucleus is the higher form.

Thus it appears that in the same proportion as animals occupy a higher position in the scale of beings, so have they both a larger quantity and a higher quality of blood. Their position in the scale is determined by the development of the central nervous system, in adaptation to which, more or less directly, the other systems relating to the life of the individual are adjusted. The adjustment of the characters of the organic life to the central nervous system is effected through the intervention of the blood, to the formation of which all the organs of that life minister, and which we may therefore regard as the highest member of the parts concerned in the organic life, in the same sense as we regard the brain as the highest of the organs of the animal life. And this eminence of the blood is shewn, first, by its chemical composition, which, as we have seen, is more highly organic than that of the greater part of the tissues; secondly, by the time at which it first appears in the embryo, in which, as the brain and spinal cord precede, in their rudiments, the other and subordinate organs of animal life, so the blood appears before any of the persistent organs of the organic life; thirdly, by the complexity and number of the processes though which it is elaborated, including all those the history of which is now to be traced till we come to that of the Nervous System.

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## CHAPTER V.

### CIRCULATION OF THE BLOOD.

THE purposes which have been assigned to the blood, those, namely, of conveying oxygen and nutritive materials to the several parts of the body, and of carrying away from them to excretory organs their refuse matters,—require that it should be constantly moving through all the parts, and at certain periods should be exposed to the atmosphere, in order that it may imbibe oxygen, and emit carbonic acid and water,

the compounds into which the principal refuse matter is converted. To this end it is provided, in man and all warm-blooded animals, that all the blood which has passed once through the several parts of the body, shall traverse the lungs, and be exposed to the atmosphere before it again takes the same course. This is effected by what is called a double circulation, or, more properly, a single complete circulation in two nearly separate parts; the organs for which are, a heart, with two separated compartments or sides, and arteries and veins so connected with each compartment of the heart, that the arteries proceeding from the one may lead to the veins belonging to the other. The course through which blood moves in such a circulation may be thus briefly described. Commencing, we will suppose, at the left ventricle of the heart, blood is impelled into the aorta and along its successive branches, the *systemic arteries*, through which all the organs of the body, except the finer textures of the lungs, derive all their blood. Through these arteries it is conveyed into the *systemic capillaries*, the minute vessels which lie intermediately between the arteries and veins of every part, and in which the blood is brought most nearly into contact with the very substance of the organs. From these, it passes into the *systemic veins*, through the main trunks of which, the *venæ cavæ*, it flows into the right auricle, and thence into the right ventricle of the heart. This completes what is called the *systemic circulation*, or systemic or general part of the circulation. In the right ventricle the blood enters the *pulmonary* or lesser circulation, in which it passes from the right ventricle through the pulmonary artery, and its branches in the lungs, to the capillaries, in which it is brought nearest to the atmosphere. From the pulmonary capillaries the blood enters, in converging streams, the pulmonary veins, which carry it to the left auricle, whence, having thus traversed the pulmonary part of the circulation, it passes again into the left ventricle, where, in the case here supposed, it started on its course.

The blood in the left ventricle is arterial (see p. 35, etc.),

and charged with oxygen in greater proportion than carbonic acid, as well as with materials for the supply of the organs. So it remains in all the systemic arteries; but in the systemic capillaries it parts with portions of those materials, and its oxygen is, in great measure, consumed in uniting with the hydrocarbonous and other substances which enter the blood-vessels from the refuse matter of the tissues. Thus the blood acquires the venous character; and in this state it traverses the systemic veins, the right side of the heart, and the pulmonary arteries; but in the pulmonary capillary vessels, emitting carbonic acid and water, and imbibing oxygen, it becomes again arterial, and so passes on to the left ventricle.

A subordinate kind of circulation is inserted in the liver, and is called the *portal circulation.* The veins belonging to that part of the systemic vessels which is appropriated to the organs of digestion, form a common trunk, called *vena portæ;* and this, instead of joining at once with the other main trunks of the systemic veins, enters the substance of the liver. There the vena portæ, branching like an artery, carries its share of the blood into capillaries, through which it passes into the hepatic veins, then goes through their largest branches into the vena cava inferior, one of the two main trunks of the systemic venous system, where the portal circulation terminates by mingling its blood with that which, in the vena cava inferior, has nearly reached the end of the systemic circulation.

The principal force provided for constantly moving the blood through this course, is that of the muscular substance of the heart; other assistant forces are those of the elastic walls of the arteries, the pressure of the muscles among which some of the veins run, the movements of the walls of the chest in respiration, and probably, to some extent, the interchange of relations between the blood and the tissues, which ensues in the capillary system during the nutritive processes. The right direction of the blood's course is determined and maintained by valves placed between each auricle and ventricle of the heart, at the orifices of communication between the ventricles

and the main arterial trunks, and in most of the veins; which valves open to permit the movement of the blood in the course described, but close when any force tends to move it in the contrary direction. We shall consider separately each member of the system of organs for the circulation: and first—

### THE ACTION OF THE HEART.

The heart's action in propelling the blood consists in the successive alternate contractions and dilatations of the muscular walls of its two auricles and two ventricles. The auricles contract simultaneously; so do the ventricles; their dilatations also are severally simultaneous; and the contractions of the one pair of cavities are synchronous with the dilatations of the other.

The description of the action of the heart may best be commenced at that period in each action which immediately precedes the beat of the heart against the side of the chest, and, by a very small interval more, precedes the pulse at the wrist. For at this time, which corresponds with the pause between the two sounds of the heart, the whole heart is in a passive state; the walls of both auricles and ventricles are relaxed, and their cavities are being dilated. The auricles are gradually filling with blood flowing into them from the veins; and a portion of this blood passes at once through them into the ventricles, the opening between the cavity of each auricle and that of its corresponding ventricle being, during all the pause, free and patent. The auricles, however, receiving more blood than at once passes through them to the ventricles, become, near the end of the pause, fully distended; then, in the end of the pause, they contract and empty their contents into the ventricles. The contraction of the auricles is sudden, and very quick; it commences at the entrance of the great veins into them, and is thence propagated towards the auriculo-ventricular opening; but the last part which contracts is the auricular appendix. The effect of this contraction of the auricles is to propel nearly

the whole of their blood into the ventricles. The reflux of blood into the great veins, is hindered by the simultaneous contraction of the muscular coats with which they are provided for some distance before their entrance into the auricles: a contraction, which, however, is not so complete but that a small quantity of blood does regurgitate, *i.e.*, flow backwards into the veins, at each auricular contraction. The effect of this regurgitation from the right auricle is limited by the valves at the junction of the subclavian and internal jugular veins, beyond which the blood cannot move backwards; and the coronary vein is preserved from it by a valve at its mouth.

The blood which is thus driven, by the contraction of the auricles, into the corresponding ventricles, being added to that which had already flowed into them during the heart's pause, is sufficient to complete the distension of the ventricles. Thus distended, they immediately contract: so immediately, indeed, that their contraction looks as if it were continuous with that of the auricles. They contract much more slowly than the auricles, and simultaneously in every part, the whole wall of each ventricle being drawn up uniformly towards the origin of the artery at its base, diminishing the cavity in every diameter, but especially in length, so that the heart assumes a shorter and more globular form than it had in the relaxed and distended state of the ventricles. In this complete and uniform contraction, the ventricles probably always thoroughly empty themselves, differing in this respect from the auricles, in which, even after their completest contraction, a small quantity of blood remains. The form and position of the fleshy columns on the internal walls of the ventricle appear, indeed, especially adapted to produce this obliteration of their cavities during their contraction; and the completeness of the closure may often be observed on making a transverse section of a heart shortly after death, in any case in which the contraction of the *rigor mortis* is very marked. In such a case only a central fissure may be discernible to the eye in the place of the cavity of each ventricle.

At the same time that the walls of the ventricles contract, the fleshy columns contract also, and bring the margins of the auriculo-ventricular valves into apposition, so that they close the auriculo-ventricular openings, and prevent the backward passage of the blood into the auricles. The whole force of the ventricular contraction is thus directed to the propulsion of the blood through their arterial orifices. During the time which elapses between the end of one contraction of the ventricles and the commencement of another, the communication between them and the great arteries—the aorta on the left side, the pulmonary artery on the right—is closed by the three semilunar valves situated at the orifice of each vessel. But the force with which the current of blood is propelled by the contraction of the ventricle separates these valves from their contact with each other and presses them back against the sides of the artery, making a free passage for the stream of blood. Then, as soon as the ventricular contraction ceases, the elastic walls of the distended artery recoil, and by pressing the blood behind the valves force them down towards the centre of the vessel, and spread them out so as to close the orifice and prevent any of the blood flowing back into the ventricles.

As soon as the contraction of the auricles is completed, they begin again to dilate, and to be filled again with blood which flows into them in a steady stream through the great venous trunks. They are thus filling during all the time in which the ventricles are contracting; and the contraction of the ventricles being ended, they also again dilate and receive again the blood that flows into them from the auricles. By the time that the ventricles are thus from one-third to two-thirds full, the auricles are distended; these, then suddenly contracting, fill up the ventricles as already described. Thus the action of the auricles consists in a succession of quick contractions and slow dilatations; that of the ventricles in a succession of contractions and dilatations of nearly equal length. Of the period occupied by a complete action of the heart, the auricles are

engaged for about one-eighth in contraction, and seven-eighths in dilating and receiving blood; while the ventricles are occupied for one-half in contracting, and the other in dilating.

The following table will explain the order of the actions already described, and their coincidences with the sounds and impulse of the heart, of which we shall next speak. It supposes the period occupied by a complete set of the actions of the heart to be divided into eight parts, and if the case be taken of a person with a pulse beating sixty times a minute, these parts may represent eighths of a second.

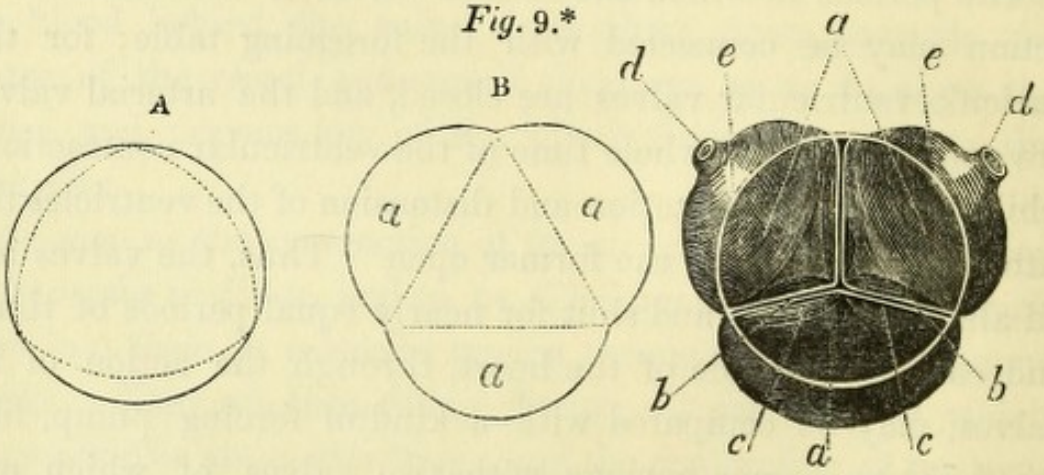
| | Eighths of a second. | |
|---|---|---|
| Last part of the pause | 1 | Aur. contracting: ventr. distended. |
| 1st sound and impulse | 4 | Ventr. contracting: aur. dilating. |
| 2nd sound | 2 | Ventr. dilating: aur. dilating. |
| Pause | 1 | Ventr. dilating: aur. distended. |

*Action of the Valves of the Heart.*

The periods in which the several valves of the heart are in action may be connected with the foregoing table; for the auriculo-ventricular valves are closed, and the arterial valves are open during the whole time of the ventricular contraction; while, during the dilatation and distension of the ventricles the latter valves are shut, the former open. Thus, the valves are all alternately open and shut for nearly equal periods of time; and each half or side of the heart, through the action of its valves, may be compared with a kind of forcing pump, like the common enema-syringe with two valves, of which one admits the fluid on raising the piston, but is closed again when the piston is forced down; while the other opens for the escape of the fluid, but closes when the piston is raised, so as to prevent the regurgitation of the fluid already forced through it. The ventricular dilatation is here represented by the raising-up of the piston; the valve thus admitting fluid represents the auriculo-ventricular valve, which is closed again when the piston is forced down, *i.e.*, when the ventricle contracts, and the other, *i.e.*, the arterial, valve opens.

The *arterial, semilunar,* or *sigmoid* valves are, as already said, brought into action by the pressure of the arterial blood forced back towards the ventricles, when the elastic walls of the arteries recoil after being dilated by the blood propelled into them in the previous contraction of the ventricle. The dilatation of the arteries is, in a peculiar manner, adapted to bring the valves into action. The lower borders of the semilunar valves are attached to the inner surface of a tendinous ring, which is, as it were, inlaid, at the orifice of the artery, between the muscular fibres of the ventricle, and the elastic fibres of the walls of the artery. The tissue of this ring is tough, and does not admit of extension under such pressure as it is commonly exposed to; the valves are equally inextensile, being formed of tough, close-textured, fibrous tissue, with strong-interwoven cords, and covered with epithelium. Hence, when the ventricle propels blood through the orifice and into the canal of the artery, the lateral pressure which it exercises

*Fig.* 9.*

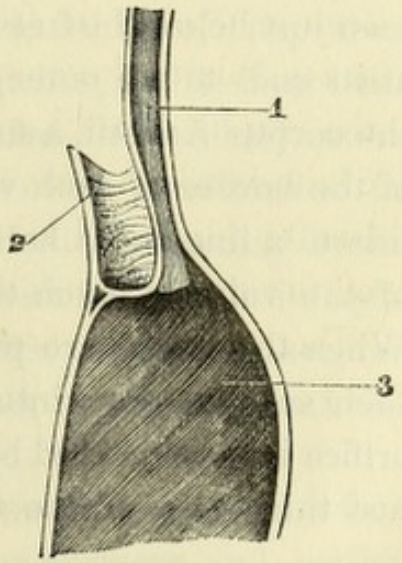



* Fig. 9.—Sections of aorta, to show the action of the semilunar valves. A. is intended to shew the valves, represented by the dotted lines, in contact with the arterial walls, represented by the continuous outer line. B. (after Hunter) shews the arterial wall distended into three pouches (*a*); and drawn away from the valves which are straightened into the form of an equilateral triangle, as represented by the dotted lines. C. (after Retzius, cxii.) shews the margins of the valves when in action; *a.* the pouches between the valves and the arterial wall; *b.* the apposed edges, *c.* the apposed surfaces, of the valves; *d.* mouths of coronary arteries; *e.* cut edge of aorta.

is sufficient to dilate the walls of the artery, but not enough to stretch in an equal degree, if at all, the unyielding valves and the ring to which their lower borders are attached. The effect, therefore, of each such propulsion of blood from the ventricle is, that the wall of the first portion of the artery is dilated into three pouches behind the valves, while the free margins of the valves, which had previously lain in contact with the inner surface of the artery (as at A, fig. 9), are drawn inwards towards its centre (fig. 9, B). Their positions may be explained by the foregoing diagrams, in which the continuous lines represent a transverse section of the arterial walls, the dotted ones the edges of the valves, first, when the valves are in contact with the walls (A), and, secondly, when the walls being dilated the valves are drawn away from them (B).

This position of the valves and arterial walls is retained so long as the ventricle continues in contraction; but, as soon as it relaxes, and the dilated arterial walls can recoil by their elasticity, they press the blood as well towards the ventricles as onwards in the course of the circulation. Part of the blood thus pressed back lies in the pouches (*a*, fig. 9, B) between the valves and the arterial walls; and the valves are by it pressed together till their margins meet in three lines radiating from the centre to the circumference of the artery, as in C, fig. 9.

*Fig.* 10.*




In an interesting paper lately read before the Royal Society (ccv.), Mr. Savory has clearly shewn that this pressure of the blood is not entirely sustained by the valves alone, but in part by the muscular substance of the ventricle. Availing himself of a method of dissection hitherto

* Fig. 10.—Vertical section through the aorta at its junction with the left ventricle. 1. Section of arterial coat. 2. Section of valve. 3. Section of ventricle.

apparently overlooked, namely, that of making vertical sections (fig. 10) through various parts of the tendinous rings, he has been enabled to show clearly that the aorta and pulmonary artery, expanding towards their termination, are situated upon the *outer* edge of the thick upper border of the ventricles, and that consequently the portion of each semilunar valve adjacent to the vessel passes over and rests upon the muscular substance — being thus supported, as it were, on a kind of muscular floor formed by the free border of the ventricle. The result of this arrangement will be, that the reflux of the blood will be most efficiently sustained by the ventricular wall, which, at the moment of its occurrence, is probably in a state of contraction.*

The effect of the blood's pressure on the valves is, as said, to cause their margins to meet in three lines radiating from the centre to the circumference (fig. 9, c). The contact of the valves in this position, and the complete closure of the arterial orifice, are secured by a peculiar construction of their borders. Among the cords which are interwoven in the substance of the valves, are two of greater strength and prominence than the rest; of which one extends along the free border of each valve, and the other forms a double curve or festoon just below the free border. Each of these cords is attached at its ends to the outer angles of its valve, and in the middle to the corpus Arantii, a small mass of fibrous tissue at the centre of the border of each valve; they thus enclose a space from a line to a line and a half in width, in which space the substance of the valve is much thinner and more pliant than elsewhere. When the valves are pressed down, all these parts or spaces of their surfaces come into contact, and the closure of the arterial orifice is thus secured by the apposition not of the mere margins and thin edges of the valves, but of all those parts of the

* Mr. Savory's preparations, illustrating this and other points in relation to the structure and functions of the valves of the heart, are in the museum of St. Bartholomew's Hospital.

surfaces of each, which lie between the free edges and the cords next below them (see fig. 9, c, *c.*) These parts are firmly pressed together, and the greater the pressure that falls on them, the closer and more secure is their apposition. The corpora Arantii meet at the centre of the arterial orifice when the valves are down, and they probably assist in the closure; but they are not essential to it, for, not unfrequently, the valves of the pulmonary artery have none, but are extended in larger, thin flapping margins. In this form of valves, also, the inlaid cords are less distinct than in those with corpora Arantii; yet the closure by contact of their surfaces is not less secure.

The *auriculo-ventricular valves*, like those already described, secure the closure of the orifices at which they are placed, by the contact of parts of their surfaces; but in most other respects their mode of action is peculiar. The valve between the right auricle and ventricle is named *tricuspid*, because it presents three principal cusps or pointed portions, and that between the left auricle and ventricle *bicuspid* or *mitral* because it has two such portions. But in both valves there is between each two principal portions a smaller one; so that more properly, the tricuspid may be described as consisting of six, and the mitral of four, portions. Each portion is of triangular form, its apex and sides lying free in the cavity of the ventricle, and its base being fixed to a tendinous ring, which encircles the orifice between the auricle and ventricle, and receives the insertions of the muscular fibres of both. In each principal portion may be distinguished a middle-piece, extending from its base to its apex, and including about half its width; this piece is thicker, and much tougher and tighter than the border-pieces which are attached loose and flapping at its sides.

While the bases of the several portions of the valves are fixed to the tendinous rings, their ventricular surfaces and borders are fastened by slender *tendinous cords* to the walls of the ventricles or to muscular columns or processes (*carneæ columnæ*) projecting from the walls into the cavities of the ventricles. In

each ventricle there are as many of these columns as there are principal portions in the corresponding valve. Of the tendinous cords, besides some which pass from the walls of the ventricle and the fleshy columns to the tendinous ring, there are some, of principal strength, which pass from the same parts to the edges of the middle pieces of the several chief portions of the valve. The ends of these cords are spread out in the substance of the valve, giving its middle piece its peculiar strength and toughness; and from these sides numerous other more slender and branching cords are given off, which are attached all over the ventricular surface of the adjacent border-pieces of the principal portions of the valves, as well as to those smaller portions which have been mentioned as lying between each two principal ones. Moreover, the muscular columns are so placed that from the summit of each, tendinous cords may proceed to the adjacent halves of two of the principal divisions, and to one intermediate or smaller division, of the valve.

During auricular contraction, the force of the blood propelled into the ventricle is transmitted in all directions, but being insufficient to raise the semilunar valves, it is expended in distending the ventricle, and in raising and gradually closing the auriculo-ventricular valves, which, when the ventricle is full, form a complete septum between it and the auricle (Halford). When the ventricle contracts, the edges of the valves are maintained in apposition by the simultaneous contraction of the fleshy columns, which are enabled thus to act by the arrangement of their tendinous cords just mentioned. In this position the segments of the valves are held secure, even though the form and size of the orifice and the ventricle may change during the continued contraction; for the border pieces are held by their mutual apposition and the equal pressure of the blood on their ventricular surfaces; and the middle pieces are secure by their great strength, and by the attachment of the tendinous cords along their margins, these cords being always held tight by the contraction of the muscular columns. A

peculiar advantage, derived from the projection of these columns into the cavity of the ventricle, seems to be, that they prevent the valve from being everted into the auricle; for, when the ventricle contracts, and the parts of its walls to which, through the medium of the columns, the tendinous cords are fixed, approach the base of the heart and the auriculo-ventricular orifices, there would be a tendency to slackness of the cords, and the valves might be everted, if it were not that while the wall of the ventricle is drawn towards the orifice, the end of the simultaneously contracting fleshy column is drawn away from it, and the cords are held tight.

What has been said applies equally to the auriculo-ventricular valves on both sides of the heart, and of both alike the closure is generally complete every time the ventricles contract. But in some circumstances, the closure of the tricuspid valve is not complete, and a certain quantity of blood is forced back into the auricle: and, since this may be advantageous, by preventing the over-filling of the vessels of the lungs, it has been called the *safety-valve action* of this valve (Hunter, Wilkinson King). The circumstances in which it usually happens are those in which the vessels of the lung are already full enough when the right ventricle contracts, as *e.g.*, in certain pulmonary diseases, in very active exertion, and in great efforts. In these cases, perhaps, because the right ventricle cannot contract quickly or completely enough, the tricuspid valve does not completely close, and the regurgitation of blood may be indicated by a pulsation in the jugular veins synchronous with that in the carotid arteries.

### *Sounds and Impulse of the Heart.*

When the ear is placed over the region of the heart, two sounds may be heard at every beat of the heart, which follow in quick succession, and are succeeded by a pause or period of silence. The first sound is dull and prolonged; its commencement coincides with the impulse of the heart, and just precedes

the pulse at the wrist. The second is a shorter and sharper sound, with a somewhat flapping character, and follows close after the arterial pulse. If the period of time occupied by the two sounds, and by the subsequent pause,—which together constitute the *rhythm* of the heart,—be divided into four equal parts, the first sound, and the very short interval between it and the second, will be found to occupy the first two parts, or half the period of the rhythm; the second sound rather less than another part, and the pause rather more than the fourth part.

The events which correspond, in point of time, with the first sound, and which may therefore contribute to its production, or to morbid changes in its characters, are (as expressed in the table at page 79) the contraction of the ventricles, the first part of the dilatation of the auricles, the closure of the auriculo-ventricular valves, the openness of the semilunar valves, and the propulsion of blood into the arteries. The sound is succeeded, in about one-thirtieth of a second, by the pulsation of the facial artery, and in about one-sixth of a second, by the pulsation of the arteries at the wrist. The second sound, in point of time, immediately follows the cessation of the ventricular contraction, and corresponds (as the same table shews) with the closure of the semilunar valves, the continued dilatation of the auricles, the commencing dilatation of the ventricles, and the opening of the auriculo-ventricular valves. The pause immediately follows the second sound, and corresponds in its first half with the completed distension of the auricles, and in its second with their contraction, and the distension of the ventricles, the auriculo-ventricular valves being all the time open, and the arterial valves closed.

Few subjects have been investigated with greater care than that relating to the *cause of the sounds of the heart*, yet, although nearly all observers agree about the cause of the *second* of these sounds, there is still great discrepancy of opinion respecting the real agent concerned in the production of the *first* sound. According to some, the first sound is due almost entirely to the noise or *bruit*, resulting from the sudden and

forcible contraction of the large mass of muscular fibres composing the walls of the two ventricles. By others it is referred exclusively to the vibrations of the auriculo-ventricular valves suddenly rendered tense by the backward pressure of blood against them. According to a third opinion, the sound results from the combined effect of both these agencies, aided also by several other attendant circumstances.

The influence of muscular bruit in producing the first sound of the heart, has doubtless been exaggerated. By many, indeed, the existence of any sound resulting from muscular contraction is questioned, by some it is entirely denied, while by others, on the contrary, it is believed to be very considerable. On the whole, perhaps, it may be concluded that the share which muscular contraction takes in the production of the first sound is not great.

The second theory, maintaining the valvular origin of the first sound, long ago advanced by Dr. Billing, has of late met with a strenuous advocate in Dr. G. B. Halford (ccxxv). There can be little doubt of its general correctness, for it is quite intelligible that the auriculo-ventricular valves suddenly rendered tense by the backward pressure of blood against them during ventricular contraction, will be thrown into vibration, and, in vibrating, will produce sound. This view is supported by the fact observed by Valentin (iv. Bd. i. p. 427), that if a portion of a horse's intestine, tied at one end, be moderately filled with water without any admixture of air, and have a syringe containing water fitted to the other end, the first sound of the heart is exactly imitated by forcing in more water, and thus suddenly rendering the walls of the intestine more tense. That the tension and vibration of the valves result principally from the forcible impulse of the blood against them, seems to be proved, from the fact of the almost complete cessation of sound when the entrance of blood into the heart is prevented by the simultaneous compression of the pulmonary veins and venæ cavæ, as in one of Dr. Halford's ingenious experiments. This experiment however, although it proves the large share which the valves, rendered tense by the blood's sudden pressure

against them, take in producing the first sound, does not demonstrate that the first sound is due solely to this cause. For exclusion of blood from the heart, not only interferes with vibration of the valves, but precludes any sound which might originate either from vibration of the blood itself, in its rapid propulsion from the ventricles, or from impulse of the walls of the distended ventricles against the parietes of the chest, or from muscular contraction,—for having nothing to contract upon, there can be no vigorous action of the walls of the ventricles; and, lastly, it precludes the possibility of sound being generated in the walls of the ventricles and the arterial coats, all of which, as well as the auriculo-ventricular valves, are rendered tense and susceptible of vibration at the time of the ventricular contraction.

Probably, therefore, the safest theory to be at present adopted with regard to the first sound of the heart, is that which admits the co-operation of several coincident agencies in its production. The principal of these agencies appears to be the state of vibration induced, especially in the auriculo-ventricular valves, also in the ventricular walls, and the coats of the aorta and pulmonary artery, all of which parts are suddenly put into a state of tension and stretching at the moment of ventricular contraction. Of the accessory causes, muscular bruit, vibration of the blood itself in its rapid compression and ejection from the heart into the arteries, with the coincident throwing-back of the semilunar valves, and the impulse of the organ against the walls of the chest, are probably the chief; though the share these severally take in the production of the first sound is still undetermined. That the heart's impulse against the chest may increase or modify the sound, is rendered probable from the fact, that when this impulse is prevented, as in cases of congenital or artificial exposure of the heart, the intensity of the first sound is said to be diminished. Under ordinary circumstances, however, the influence of this cause of sound is probably very slight, for the impulse then consists rather of a general bulging of the walls of the ventricles, than an actual

*blow* or concussion against the chest: but in disease it is often more manifest.

The cause of the *second* sound appears to be more simple than that of the first. It is probably due almost entirely to the sudden tightening of the semilunar valves when they are pressed down across the orifice of the aorta and pulmonary artery; for, of the other events which take place during the second sound, none is calculated to produce sound. The influence of the valves in producing the sound, is illustrated by the experiment already quoted from Valentin, and by others performed on large animals, such as calves, in which the results could be fully appreciated. In these experiments two delicate curved needles were inserted, one into the aorta, and another into the pulmonary artery, below the line of attachment of the semilunar valves, and, after being carried upwards about half an inch, were brought out again through the coats of the respective vessels, so that in each vessel one valve was included between the arterial walls and the wire. Upon applying the stethoscope to the vessels, after such an operation, the second sound had ceased to be audible. Disease of these valves, when so extensive as to interfere with their efficient action, also often demonstrates the same fact, by modifying or destroying the distinctness of the second sound. The second sound does not continue all the time the semilunar valves are closed, probably because it is only produced by the tightening and soon-ending vibration of the valves.

The contraction of the auricles which takes place in the end of the pause is inaudible outside the chest, but may be heard when the heart is exposed and the stethoscope placed on it, as a slight sound preceding and continued into the louder sound of the ventricular contraction.

*The Impulse of the Heart.*—At the commencement of each ventricular contraction, the heart may be felt to beat with a slight shock or *impulse* against the walls of the chest. This impulse is most evident in the space between the fifth and sixth ribs, between one and two inches to the left of the sternum.

The force of the impulse, and the extent to which it may be perceived beyond this point, vary considerably in different individuals, and in the same individuals under different circumstances. It is felt more distinctly, and over a larger extent of surface, in emaciated than in fat and robust persons, and more during a forced expiration than in a deep inspiration; for, in the one case, the intervention of a thick layer of fat or muscle between the heart and the surface of the chest, and in the other the inflation of the portion of lung which overlaps the heart, prevents the impulse from being fully transmitted to the surface. An excited action of the heart, and especially a hypertrophied condition of the ventricles, will increase the impulse, while a depressed condition, or an atrophied state of the ventricular walls, will diminish it.

The impulse of the heart is probably the result, in part, of a tilting forwards of the apex, so that it is made to strike against the walls of the chest. This tilting movement is thought to be effected by the contraction of the spiral muscular fibres of the ventricles, and especially of certain of these fibres which, according to Dr. Reid (lxxiii. vol. ii. p. 606), arise from the base of the ventricular septum, pass downwards and forwards, forming part of the septum, then emerge and curve spirally around the apex and adjacent portion of the heart. The whole extent of movement thus produced is, however, but slight. The condition, which, no doubt contributes most to the occurrence and character of the impulse of the heart, is its change of shape; for, during the contraction of the ventricles, and the consequent approximation of the base towards the apex, the heart becomes more globular, and bulges so much, that a distinct impulse is felt when the finger is placed over the bulging portion, either at the front of the chest, or under the diaphragm (see especially Halford, ccxxv.) The production of the impulse is, perhaps, further assisted by the tendency of the aorta to straighten itself and diminish its curvature when distended with the blood impelled by the ventricle; and, by the elastic recoil of all the parts about the base

of the heart, which, according to the experiments of Kürschner (xv. Art. *Herzthätigkeit*), are stretched downwards and backwards by the blood flowing into the auricles and ventricles during the dilatation of the latter, but recover themselves when, at the beginning of the contraction of the ventricles, the flow through the auriculo-ventricular orifices is stopped. But these can be only accessory conditions in the perfect state of things: for the same tilting movement of the heart ensues when its apex is cut off, and no tension or change of form can be produced by the blood.

### *Frequency and Force of the Heart's Action.*

The frequency with which the heart performs the actions we have described, may be counted by the pulses at the wrist, or in any other artery; for these correspond with the contractions of the ventricles.

The heart of a healthy adult man in the middle period of life, acts from seventy to seventy-five times in a minute. The frequency of the heart's action gradually diminishes from the commencement to the end of life, thus :—

| | |
|---|---|
| In the embryo the average number of pulses in a minute is | 150 |
| Just after birth . . . . . from | 140 to 130 |
| During the first year . . . . . | 130 to 115 |
| During the second year . . . . . | 115 to 100 |
| During the third year . . . . . | 100 to 90 |
| About the seventh year . . . . . | 90 to 85 |
| About the fourteenth year, the average number of pulses in a minute is from . . . . | 85 to 80 |
| In the middle period of life . . . . . | 75 to 70 |
| In old age . . . . . | 65 to 50 |

In persons of sanguine temperament, the heart acts somewhat more frequently than in those of the phlegmatic; and in the female sex more frequently than in the male.

After a meal its action is accelerated, and still more so during bodily exertion or mental excitement; it is slower during sleep. The effect of disease in producing temporary

increase or diminution of the frequency of the heart's action is well known. From the observation of several experimenters, it appears that, in the state of health, the pulse is most frequent in the morning, and becomes gradually slower as the day advances: and that this diminution of frequency is both more regular and more rapid in the evening than in the morning. It is found, also, that as a general rule, the pulse, especially in the adult male, is more frequent in the standing than in the sitting posture, and in the latter than in the recumbent position; the difference being greatest between the standing and the sitting posture. The effect of change of posture is greater as the frequency of the pulse is greater, and accordingly, is more marked in the morning than in the evening. Dr. Guy, by supporting the body in different postures, without the aid of muscular effort of the individual, has proved that the increased frequency of the pulse in the sitting and standing positions is dependent on the muscular exertion engaged in maintaining them; the usual effect of these postures on the pulse being almost entirely prevented when the usually attendant muscular exertion was rendered unnecessary (lviii. Nos. 6 and 7). The effect of food, like that of change of posture, is greater in the morning than in the evening. According to Parrot, the frequency of the pulse increases in a corresponding ratio with the elevation above the sea; and Dr. Frankland, who lately passed a night on the summit of Mont Blanc, informed the author that his pulse was about double the ordinary standard all the time he was there. After six hours' perfect rest and sleep at the top, it was 120, on descending to the corridor it fell to 108, at the Grands Mulets it was 88, at Chamounix 56; normally, his pulse is 60.

In health there is observed a nearly uniform relation between the frequency of the pulse and of the respirations; the proportion being, on an average, one of the latter to three or four of the former. The same relation is generally maintained in the cases in which the pulse is naturally accelerated, as after food or exercise: but in disease this relation usually

ceases to exist. In many affections accompanied with increased frequency of the pulse, the respiration is, indeed, also accelerated, yet the degree of its acceleration bears no definite proportion to the increased number of the heart's actions: and in many other cases, the pulse becomes more frequent without any accompanying increase in the number of respirations; or, the respiration alone may be accelerated, the number of pulsations remaining stationary, or even falling below the ordinary standard. (On the whole of this subject the article *Pulse*, by Dr. Guy, in the Cyclopædia of Anatomy and Physiology, may be advantageously consulted).

The *force* with which the left ventricle of the heart contracts is about double that exerted by the contraction of the right: being equal (according to Valentin) to about $\frac{1}{50}$th of the weight of the whole body, that of the right being equal only to $\frac{1}{100}$th of the same (iv. Bd. 1, p. 415, etc.). This difference in the amount of force exerted by the contraction of the two ventricles results from the walls of the left ventricle being about twice as thick as those of the right. And the difference is adapted to the greater degree of resistance which the left ventricle has to overcome, compared with that to be overcome by the right: the former having to propel blood through every part of the body, the latter only through the lungs.

The *capacity* of the two ventricles is probably exactly the same. It is difficult to determine with certainty how much this may be; but, taking the mean of various estimates, it may be inferred that each ventricle is able to contain, on the average, about three ounces of blood, the whole of which is impelled into their respective arteries at each contraction. The capacity of the auricles is rather less than that of the ventricles: the thickness of their walls is considerably less. The latter condition is adapted to the small amount of force which the auricles require, in order to empty themselves into their adjoining ventricles; the former to the ventricles being partly filled with blood before the auricles contract.

The force exercised by the auricles in their contraction has not been determined. Neither is it known with what amount of force either the auricles or the ventricles dilate: but there is no evidence for the opinion that in their dilatation they can materially assist the circulation by any such action as that of a sucking-pump, or a caoutchouc bag, in drawing blood into their cavities. That the force the ventricles exercise in dilatation is very slight was proved by Oesterreicher (c. p. 33). He removed the heart of a frog from the body, and laid upon it a substance sufficiently heavy to press it flat, and yet so small as not to conceal the heart from view; he then observed that during the contraction of the heart, the weight was raised; but that during its dilatation, the heart remained flat. And the same was shewn by Dr. Clendinning, who, applying the points of a pair of spring callipers on the heart of a live ass, found that their points were separated as often as the heart swelled up in the contraction of the ventricles, but approached each other by the force of the spring when the ventricles dilated. Seeing how slight the force exerted in the dilatation of the ventricles is, it has been supposed that they are only dilated by the pressure of the blood impelled from the auricles: but that both ventricles and auricles dilate spontaneously is proved by their continuing their successive contractions and dilatations when the heart is removed, or even when they are separated from one another, and when therefore no such force as the pressure of blood can be exercised to dilate them. By such spontaneous dilatation they at least offer no resistance to the influx of blood, and save the force which would otherwise be required to dilate them.

### *Cause of the Rhythmic Action of the Heart.*

It has been attempted in various ways to account for the existence and continuance of those peculiar rhythmic movements by which the action of the heart is distinguished from

that of all the other muscles. By some it has been supposed that the contact of arterial blood with the lining membrane of the left cavities of the heart, and of venous blood with that of the right cavities, furnishes a stimulus, in answer to which the walls of these cavities contract. And they explain the rhythmic order in which these contractions ensue, by supposing that the same act, — the systole, which expels the stimulating fluid from the ventricles, causes the auricles to be filled from the veins; and that the contraction of the auricles thereupon induced gives rise, in its turn, to the filling and consequent contraction of the ventricles. But this, and all hypotheses concerning the action of the heart which suppose the necessity of the contact of blood, or any such stimulus, are disproved by the fact that the heart, especially in Amphibia and fishes, will continue to contract and dilate regularly and in rhythmic order after it is removed from the body, completely emptied of blood, and even placed in a vacuum where it cannot receive the stimulus of the atmospheric air.

The influence of the mind, and of some affections of the brain and spinal cord upon the action of the heart, proves that it is not altogether, or at all times, independent of the cerebro-spinal nervous system. Yet the numerous experiments instituted for the purpose of determining the exact relation in which the heart stands towards this system, have failed to prove that the action is directly governed by the power of any portion of the brain or spinal cord. The results of the experiments are, in many instances, contradictory; but a general conclusion from them may be, that no uniform and decided alteration in the movements of the heart is produced by irritation of any part of either of those nervous centres. Sudden destruction of either the brain or spinal cord alone, or of both together, produces, immediately, a temporary interruption or cessation of the heart's action: but this appears to be only an effect of the *shock* of so severe an injury; for, in some such cases, the movements of the heart

are subsequently resumed, and if artificial respiration be kept up, may continue for a considerable time; and may then again be arrested by a violent shock applied through an injury of the stomach. While, therefore, we must admit an indirect or occasional influence exercised by, or through, the brain and spinal cord upon the movements of the heart, and may believe this influence to be the greater the more highly the several organs are developed, yet it is clear that we cannot ascribe the regular determination and direction of the movements to these nervous centres.

The persistence of the movements of the heart in their regular rhythmic order, after its removal from the body, and their capability of being then re-excited by an ordinary stimulus after they have ceased, prove that the cause of these movements must be resident within the heart itself. And it seems probable, from the experiments and observations of Remak (cxxx. No. ii. 1840), Volkmann (lxxx., 1844, p. 424), Dr. Robert Lee (cxxiii., 1847, and lxxi. vol. xlv. p. 224), and others (see xxv., 1844-5, p. 13), that it may be connected with the existence of numerous minute ganglia of the sympathetic nervous system, which with connecting nerve-fibres, are distributed through the substance of the heart. These ganglia appear to act as so many centres or organs for the production of motor impulse; while the connecting nerve-fibres unite them into one system, and enable them to act in concert and direct their impulses so as to excite in regular series the successive contractions of the several muscles of the heart. The mode in which ganglia thus act as centres and co-ordinators of nervous power will be described in the chapter on the Nervous System; and it will appear probable that the chief peculiarity of the heart, in this regard, is due to the number of its ganglia, and the apparently equal power which they all exercise; so that there is no one part of the heart whose action, more than another's, determines the actions of the rest. Thus, if the heart of a reptile be bisected, the rhythmic successive actions of auricle and ventricle will go on in both halves: we

therefore cannot say that the action of the right side determines or regulates that of the left, or *vice versâ*; and we must suppose that when they act together in the perfect heart, it is because they are both, as it were, set to the same time. Neither can we say that the auricles determine the action of the ventricles; for, if they are separated, they will both contract and dilate in regular, though not necessarily similar, succession. A fact pointed out by Mr. Malden shews how the several portions of each cavity are similarly adjusted to act alike, yet independently of each other. If a point of the surface of the ventricle of a turtle's or frog's heart be irritated, it will immediately contract, and very quickly afterwards all the rest of the ventricle will contract; but, at the close of this general contraction, the part that was irritated and contracted first, is slightly distended or pouched out, shewing that it was adjusted to contract in, and for only, a certain time, and that therefore as it began to contract first, so it began to dilate first.*

Mr. Paget, however, has shewn that the cause of the rhythmic motion does not exist equally in all parts of the heart. If, for example, the cut-out heart of a tortoise be divided into two pieces, one comprising the auricles and the base of the ventricle, the other comprising the rest of the ventricle, the former will continue to act rhythmically, the latter will cease to do so, and no rhythmic action can be, by any means, excited in it. Other sections of the heart and experiments of other kinds, seem to show that the cause of the rhythmic action of the ventricle, and probably also of the auricles so long as they are associated with it, is situated about the boundary-ring between the auricles and ventricle;

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* The experiment also proves the uniform and simultaneous action of the whole wall of the ventricle, and the advantage thereof; since if one part of the wall ceased to contract before the rest, it would be pouched out by the communicated pressure of the blood still compressed by the continuing contraction of the rest of the wall.

for that which remains connected with this part retains its rhythm, while that which is disconnected from it loses rhythm. They seem to prove, also, that the rhythm does not depend on the properties of the muscular tissue alone or independently, but is derived from the nervous ganglia, as so many centres of rhythmic action, which are chiefly situated in the region named. Why these nervous centres should issue impulses for rhythmic rather than for continuous action, is still a debateable point. The most philosophical interpretation yet given of it, and of rhythmic processes in general, is that by Mr. Paget, who regards them as dependent on rhythmic nutrition, *i.e.*, on a method of nutrition in which the acting parts are gradually raised, with time-regulated progress, to a certain state of instability of composition which then issues in the discharge of their functions, *e. g.*, of nerve-force in the case of the cardiac ganglia, by which force the muscular walls are excited to contraction. According to this view, there is in the nervous ganglia of the heart, and in all parts originating rhythmic processes, the same alternation of periods of action with periods of repose, during which the waste in the structure is repaired, as is observed in most of, if not all the organic phenomena of life. All organic processes seem to be regulated with exact observance of time; and rhythmic nutrition and action, as exhibited in the action of the heart, is but a well-marked example of such chronometric arrangement (cxxiii. May, 1857). Another interpretation of the rhythmic movement of the heart has been given of late by Dr. Brown-Séquard; he attributes it to irritation produced by carbonic acid in the blood circulating through the muscular tissue of the heart.

The connection of the action of the heart with the other organs, and the influences to which it is subject through them, are explicable from the connection of its nervous system with the other ganglia of the sympathetic, and with the brain and spinal cord through, chiefly, the pneumogastric nerves. But this influence is proved in a much more striking manner by the

phenomena of disease than by any experimental or other physiological observations. The influence of a shock in arresting or modifying the action of the heart,—its very slow action after compression of the brain, or injury to the cervical portion of the spinal cord,—its irregularities and palpitations in dyspepsia and hysteria,—are better evidence for the connection of the heart with the other organs through the nervous system, than are any results obtained by experiments. The best of such results are recorded by E. H. Weber (xv. Art. *Muskelbewegung*), and Professor Lister (cxxiii. vol. ix. No. 32). The former found that the electro-magnetic stimulus applied in the frog to the *bulbus arteriosus*, around which the principal fibres of the sympathetic nerves supplying the heart are placed, accelerated and strengthened the heart's action; but that applied to the pulsating part of the vena cava inferior, where are the principal filaments it derives from the pneumogastric nerves, it retarded the action. He was disposed therefore to think that, in general, stimuli conveyed through the sympathetic nerve would accelerate, and through the pneumogastric would retard, the heart's action. The latter conclusion seemed to be corroborated by the fact, also stated by him, that the heart's action is retarded by stimulus applied to any part between the corpora quadrigemina and posterior part of the fourth ventricle of the brain, or to both trunks of the pneumogastric nerves at once, or by division of both pneumogastric nerves in the necks of Mammalia. Professor Lister, however, found that if the irritation applied to the posterior part of the brain be slighter than the galvanic stimulus used by Weber, the result is an increase, rather than a retardation, of the heart's action. From this, and from other experiments, he concluded that while a powerful stimulus to the vagus retards (in consequence of the *shock* or exhaustion produced by it), slighter irritation accelerates the movements of the heart. Similar results were likewise obtained by irritation of the sympathetic branches connecting the cord with the cardiac ganglia.

### *Effects of the Heart's Action.*

That the contractions of the heart supply alone a sufficient force for the circulation of the blood appears to be established by the results of several experiments, of which the following is one of the most conclusive:—Dr. Sharpey (xciv. vol. lxiii. p. 20) injected bullock's blood into the thoracic aorta of a dog recently killed, after tying the abdominal aorta above the renal arteries, and found that, with a force just equal to that by which the ventricle commonly impels the blood in the dog, the blood which he injected into the aorta passed in a free stream out of the trunk of the vena cava inferior. It thus traversed both the systemic and hepatic capillaries; and when the aorta was not tied above the renals, blood injected under the same pressure flowed freely through the vessels of the lower extremities. A pressure equal to that of one and a-half or two inches of mercury was, in the same way, found sufficient to propel blood through the vessels of the lungs.

But although it is probably true that the heart's action alone is sufficient to ensure the circulation, yet there is reason to believe in the existence of several other forces which are, as it were, supplementary to the action of the heart, and assist it in maintaining the circulation. The principal of these supplemental forces have been already alluded to, and will now be more fully pointed out.

### THE ARTERIES.

For the purpose of explaining the influence of the arteries in the circulation it will be sufficient to consider the walls of an artery as containing, at the most, five distinct layers or coats, namely, an external, an elastic, a muscular, an internal coat, and an epithelial lining.* The *external* coat is constructed of

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* For the best account of these structures see Henle (xxxvii. p. 494), or an abstract of his observations (xxv. 1842, p. 39); also Kölliker (lix. 1847; ccvi. 1852, p. 545; ccxviii. 1860, p. 482).

ordinary fibro-cellular tissue, the fibres of which are arranged, for the most part, in a longitudinal direction. It forms a strong, tough investment, which though capable of extension, appears principally designed to strengthen the walls of the artery, and to guard against their excessive distension from the force of the heart's action. It serves another purpose also in affording a suitable tissue for the ramifications of the *vasa arteriarum*, or nutritive vessels for the supply of the arterial walls. The internal arterial coat (the striated or fenestrated coat of Henle) consists of a very thin and brittle membrane. It possesses little elasticity, and is thrown into folds or wrinkles, when an artery contracts. Its internal surface is lined with a delicate layer of epithelium, which makes it smooth and polished, and furnishes a nearly impermeable surface, along which the blood may flow with the smallest possible amount of resistance from friction.

The elastic and muscular coats are the seats of those properties by which arteries chiefly influence the circulation. Previous to the time of John Hunter, the distinction between these two coats, which constitute the chief thickness of the arterial walls appears to have been overlooked, and it was usual to describe them together as a single tissue, under the denomination of the middle, fibrous, or elastic coat. But in the admirable account which Hunter gave of the properties of arteries, proof was afforded of the dissimilarity in structure and function between the inner and outer portions of this supposed single coat. And recent observations have shown the accuracy of his account, and furnished additional facts in confirmation of it. The outer of these two coats is made up almost entirely of fibres of yellow elastic tissue, and constitutes, as Hunter named it, the *elastic* coat. The inner consists of circularly-arranged, pale, flat fibres, or "fibre-cells" of Kölliker, which differ in no essential respect from the fibres of organic muscle, such as those which compose the muscular coat of the stomach and intestines; but are mingled with more filaments of fine elastic tissue. Its chemical characters are equally similar to those of organic muscle. The older analyses, in

which the similarity was not detected, were probably made of the walls of the largest arteries in which elastic tissue alone exists. By later analysis, Dr. Retzius (cvii. vol. i. p. 171) has found in this coat a proteine-compound, which neither cellular nor elastic tissue contains; and Dr. Donders (cviii. 1846, p. 67) has proved the same more perfectly. When, he says, strong nitric acid is applied to any compound of proteine it forms with it what is termed xantho-proteinic acid, which, with ammonia, produces a yellow xantho-proteinate of ammonia. On applying this test, with the requisite cautions, to the coats of blood-vessels, he found that the muscular arterial coat alone assumed the characteristic yellow colour. The other coats, as well as all the coats of veins, remained unchanged in colour. He found also that potash acts on this inner coat of arteries, as on organic muscle, separating its fibres, making them granular, and finally dissolving them. For this coat, therefore, the name of *muscular*, applied by Hunter, may be retained.

These two coats exist in different relative degrees of thickness in different arteries; and, in general, are in an inverse ratio to each other, for the arteries which possess most elastic tissue have the least muscular tissue, while those whose walls are most muscular, are in general the least elastic. In the large arteries, such as the aorta and its main branches, scarcely a trace of the muscular coat can be found, nearly the whole thickness of their walls consisting of elastic tissue. But in the arteries farther removed from the heart, and of smaller size, the proportionate thickness of the elastic coat gradually diminishes while, as a general rule, that of the muscular coat progressively increases. Moreover, in the arteries of certain organs, probably of those in which the supply of blood is subject to greater than usual variations in adaptation to fluctuations in the amount of function they discharge, there is proportionately greater development of the muscular coat.

Of the properties which the arteries possess in these two coats, the muscularity has its seat exclusively in the muscular

coat, and no artery without this coat would present any contraction similar to that of muscles. But elasticity is a property not exclusively, though especially, seated in the elastic coat; rather, all the coats, except perhaps the internal, are in some measure elastic, and will recoil after being distended; and the effect their elasticity produces is yet further assisted by the elasticity of the tissues around them.

The *purposes of the elasticity* of arteries are chiefly twofold; 1st, To guard them from the suddenly exerted pressure to which they are subjected at each contraction of the ventricles. In every such contraction, the contents of the ventricles are forced into the arteries more quickly than they can be discharged into and through the capillaries. The blood therefore being, for an instant, resisted in its onward course, a part of the force with which it was impelled is directed against the sides of the arteries; under this force, which might burst a brittle tube, their elastic walls dilate, stretching enough to receive the blood, and as they stretch becoming more tense and more resisting. Thus, by yielding, they, as it were, break the shock of the force impelling the blood, and exhaust it before they are in danger of bursting through being overstretched. Elasticity is thus advantageous in all arteries, but chiefly so in the aorta and its large branches, which are provided, as already said, with a large quantity of elastic tissue, in adaptation to the great force of the left ventricle, which falls first on them, and to the increased pressure of the arterial blood in violent expiratory efforts.

On the subsidence of the pressure, when the ventricles cease contracting, the arteries are able, by the same elasticity, to resume their former calibre; and in thus doing, they manifest the 2nd chief purpose of their elasticity, that, namely, of equalizing the current of the blood by maintaining pressure on the blood in the arteries during the periods at which the ventricles are at rest or dilating. If some such method as this had not been adopted, if for example, the arteries had been rigid

tubes, the blood, instead of flowing as it does, in a constant stream, would have been propelled through the arterial system in a series of jerks corresponding to the ventricular contractions, with intervals of almost complete rest during the inaction of the ventricles. But in the actual condition of the arteries, the force of the successive contractions of the ventricles is expended partly in the direct propulsion of the blood, and partly in the dilatation of the elastic arteries; and in the intervals between the contractions of the ventricles, the force of the recoiling and contracting arteries is employed in continuing the same direct propulsion. Of course the pressure exercised by the recoiling arteries is equally diffused in every direction through the blood, and the blood would tend to move backwards as well as onwards but that all movement backwards is prevented by the closure of the arterial valves, which takes place at the very commencement of the recoil of the arterial walls.

By this exercise of the elasticity of the arteries, all the force of the ventricles is made advantageous to the circulation; for that part of their force which is expended in dilating the arteries, is restored in full, according to that law of action of elastic bodies, by which they return to the state of rest with a force equal to that by which they were disturbed therefrom. There is thus no loss of force; but neither is there any gain, for the elastic walls of the artery cannot originate any force for the propulsion of blood—they only restore that which they received from the ventricles; they would not contract, had they not first been dilated, any more than a spiral spring would shorten itself, unless it were first elongated. The advantage of elasticity in this regard is, therefore, not that it increases, but that it equalises or diffuses the forces derived from the periodic contractions of the ventricles. The force with which the arteries are dilated every time the ventricles contract, might be said to be received by them in store, to be all given out again in the next succeeding period of dilatation of the ventricles. It is by this equalising influence of the suc-

cessive branches of every artery that, at length, the intermittent accelerations produced in the arterial current by the action of the heart cease to be observable, and the jetting stream is converted into the continuous and equable movement of the blood which we see in the capillaries and veins.

Two other purposes served by the elasticity of arteries, must not be overlooked. One is the capacity which the arteries have, for receiving more than the average quantity of blood, both every time the ventricles contract, and when the supply of blood to the whole body or any part of it is, for a time, unusually large. In all such cases, the enlargement of the arteries is effected by increase of both their diameter and their length; and the elongation appears to be, generally, more considerable than the dilatation. The other purpose served by the elasticity is, that by means of it the arteries are enabled to adapt themselves to the different movements of the several parts of the body.

The evidence for the *muscularity* of arteries may be given at some length. We have already referred to Mr. Hunter's account of the muscular structure of the inner layer of the middle coat of all but the largest arteries, and to the fact, first observed by Henle, that this layer is composed of fibres in all respects similar to those of organic muscle, though mingled with fine elastic filaments. The observation of the action of arteries will show, 1st, the operation of a contractile power in arteries, essentially distinct from their elasticity; and, 2ndly, the identity of this power with muscular contractility.

When a small artery in the living subject is exposed to the air or cold, it gradually but manifestly contracts. Hunter (i. vol. iii. p. 157) observed that the posterior tibial artery of a dog when laid bare, became in a short time so much contracted as almost to prevent the transmission of blood; and the observation has been often and variously confirmed. Simple elas-

ticity could not effect this; for after death, when the vital muscular power has ceased, and the mechanical elastic one alone operates, the contracted artery dilates again.

When an artery is cut across, its divided ends contract, and the orifices may be completely closed. The rapidity and completeness of this contraction are different in different animals; they are generally greater in young than in old animals; and less, apparently, in man than in animals. In part this contraction is due to elasticity, but in part, no doubt, to muscular action; for it is generally increased by the application of cold, or of any simple stimulating substances, or by mechanically irritating the cut ends of the artery, as by pricking or twisting them. Such irritation would not be followed by these effects, if the arteries had no other power of contracting than that depending upon elasticity.

The contractile property of arteries continues many hours after death, and thus affords an opportunity of distinguishing it from elasticity. When a portion of an artery, for example the splenic artery, of a recently killed animal, is exposed, it gradually contracts, and its canal may be thus completely closed: in this contracted state it remains for a time, varying from a few hours to two days: then it dilates again, and permanently retains the same size. If, while contracted, the artery be forcibly distended, its contractility is destroyed and it holds a middle or natural size.

This persistence of the contractile property after death was well shown in an observation of Hunter, which may be mentioned as proving also the greater degree of contractility possessed by the smaller than by the larger arteries. Having injected the uterus of a cow, which had been removed from the animal upwards of twenty-four hours, he found, after the lapse of another day, that the larger vessels had become much more turgid than when he injected them, and that the smaller arteries had contracted so as to force the injection back into the larger ones.

The results of an experiment which Hunter made with

the vessels of an umbilical cord, prove, still more strikingly, the long continuance of the contractile power of arteries after death. In a woman delivered on a Thursday afternoon, the umbilical cord was separated from the fœtus, having been first tied in two places, and then cut between, so that the blood contained in the cord and placenta was confined in them. On the following morning, Hunter tied a string round the cord, about an inch below the other ligature, that the blood might still be confined in the placenta and remaining cord. Having cut off this piece, and allowed all the blood to escape from its vessels, he attentively observed to what size the ends of the cut arteries were brought by the elasticity of their coats, and then laid aside the piece of cord to see the influence of the contractile power of its vessels. On Saturday morning, the day after, the mouths of the arteries were completely closed up. He repeated the experiment the same day with another portion of the same cord, and on the following morning found the results to be precisely similar. On the Sunday, he performed the experiment the third time, but the artery then seemed to have lost its contractility, for on the Monday morning, the mouths of the cut arteries were found open. In each of these experiments there was but little alteration perceived in the orifices of the veins (i. vol. iii. p. 158.)

The influence of cold in increasing the contraction of a divided artery has been referred to: it has been shewn, also, by Schwann, in an experiment on the mesentery of a living toad. Having extended the mesentery under the microscope, he placed upon it a few drops of water, the temperature of which was some degrees lower than that of the atmosphere. The contraction of the vessels soon commenced, and gradually increased until, at the expiration of ten or fifteen minutes, the diameter of the canal of an artery, which at first was 0·0724 of an English line, was reduced to 0·0276. The arteries then dilated again, and at the expiration of half an hour had acquired nearly their original size. By renewing the application of the water, the contraction was reproduced: in this way

the experiment could be performed several times on the same artery. The veins did not contract. It is thus proved that cold will excite contraction in the walls of very small, as well as of comparatively large arteries: it could not produce such contraction in a merely elastic substance; but it is a stimulus to the organic muscular fibres in many other parts, as well as in the arterial coat; as, *e.g.*, in the skin, the dartos, and the walls of the bronchi.

Lastly, satisfactory evidence of the muscularity of the arterial coats is furnished by the experiments of Ed. and E. H. Weber (lxxx. 1847, p. 232), and of Professor Kölliker (cxc. July, 1850, p. 241), in which they applied the stimulus of electro-magnetism to small arteries. One principal circumstance which induced Müller to deny the muscularity of arteries, was the seeming impossibility of producing contractions in arteries by galvanic and electric stimuli, which excite all true muscular tissues to manifest contraction. An explanation of the failure may be found in the circumstance that, in nearly all the experiments, the arteries examined were of large size, such as the aorta and the carotid, in which there is little or no muscular tissue. The experiments of the Webers were performed on the small mesenteric arteries of frogs; and the most striking results were obtained, when the diameter of the vessels examined did not exceed from $\frac{1}{7}$ to $\frac{1}{17}$ of a Paris line. When a vessel of this size was exposed to the electric current, its diameter, in from five to ten seconds, became one-third less, and the area of its section about one-half. On continuing the stimulus, the narrowing gradually increased, until the calibre of the tube became from three to six times smaller than it was at first, so that only a single row of blood-corpuscles could pass along it at once; and eventually the vessel was closed and the current of blood arrested.

Thus, with the exception of the largest trunks, the arteries appear to offer every necessary evidence of muscularity. One of their coats has the structure and chemical composition of organic muscle; and, like such muscle, they contract on expo-

sure, on division and mechanical irritation, after death with a kind of *rigor mortis*, on the application of cold, and under the stimulus of electricity: in all these contractions they are reduced to a size less than that which their mere elasticity would give them, and from all they are commonly, after a time, again by their elasticity restored to a larger size.

With regard to the *purpose served by the muscular coat* of the arteries, there appears no sufficient reason for supposing that it, in any way, assists in propelling the onward current of blood. It could not do so unless it possessed the property of alternately contracting and relaxing coincidently with the relaxation and contraction of the ventricles; or unless it had a kind of peristaltic or vermicular movement commencing at the heart, and thence propagating itself rapidly along the several arteries; but there is no evidence to shew that the arteries ever contract in either of these modes. The most probable office of the muscular coat is that of regulating the quantity of blood to be received by each part, and of adjusting it to the requirements of each, according to various circumstances, but chiefly and most naturally, according to the activity with which the functions of each part are at different times performed. The amount of function discharged by each organ of the body varies at different times, and the variations often quickly succeed each other, so that, like the brain for example, during sleep and waking, within the same hour a part may be now very active and then inactive. In all its active exercise of function, such a part requires a larger supply of blood than is sufficient for it during the times when it is comparatively inactive. It is evident that the heart cannot regulate the supply to each part at different periods, neither could it be regulated by any general and uniform contraction of the arteries; but it may be regulated by the power which the arteries of each part have, in their muscular coat, of contracting so as to diminish, and of passively dilating or yielding so as to permit an increase of, the supply of blood, according as the requirements of the part may demand. And thus, while the ventricles of the heart

determine the total quantity of blood to be sent onwards at each contraction, and the force of its propulsion, and while the large and merely elastic arteries distribute it and equalise its stream, the smaller arteries with muscular coats add to these two purposes, that of regulating and determining, according to its requirements, the proportion of the whole quantity of blood which shall be distributed to each part.

The contraction of an artery may also be regarded as fulfilling a natural purpose when, the artery being cut, it first limits and then arrests the escape of blood. It is only because of such contraction that we are free from danger through even very slight wounds; for it is only when the artery is closed that the processes for the more permanent and secure prevention of bleeding are established.

There are occasions in which the whole of the arteries appear to be contracted; such are those of diseases attended with a small hard pulse, but they probably occur only in morbid conditions, and physiology appears incapable of explaining them.

The normal contraction of arteries is probably excited through the instrumentality of the nerve-fibres of the sympathetic system distributed in their walls, and connected through the medium of ganglia with the fibres supplying the organ to which such arteries convey blood.

From what has been said in the preceding pages, it appears that the office of the arteries in the circulation is, 1st, the conveyance and distribution of blood to the several parts; 2nd, the equalization of the current, and the conversion of the pulsatile jetting movement given to the blood by the ventricles, into the uniform flow; 3rd, the regulation of the supply of blood to each part, in accordance with its demands. In explanation of the mode in which, by the combination of the elastic and muscular coats of arteries, this three-fold office is accomplished, we may use, as a summary of what has been already said, the words of Mr. Hunter, who observes that, "there are three states

in which an artery is found, viz., 1st, the natural pervious state; 2nd, the stretched; and 3rd, the contracted state, which may or may not be pervious. The natural pervious state is that to which the elastic power naturally brings a vessel which has been stretched beyond or contracted within the extent which it held in a state of rest. The stretched is that state produced by the impulse of the blood in consequence of the contraction of the heart: from which it is again brought back to the natural state by the elastic power, perhaps assisted by the muscular. The contracted state of an artery arises from the action of the muscular power, and it is again restored to the natural state by the elastic" (i. vol. iii. p. 159).

It must be observed, however, that the natural pervious state of an artery, here spoken of, is not one of absolute *rest;* for Mr. Savory has shown that the natural state of all arteries, in regard at least to their length, is one of tension—that they are always more or less stretched, and ever ready to recoil by virtue of their elasticity, whenever the opposing force is removed. The extent to which the divided extremities of arteries retract is a measure of this tension, not of their elasticity (ccxxxii.).

## *The Pulse.*

The jetting movement of the blood which, as just stated, it is one of the offices of the arteries to change and put an end to, is the cause of *the pulse,* and therefore needs a separate consideration. We have already said, that as the blood is not able to pass through the arteries so quickly as it is forced into them by the ventricle, on account of the resistance it experiences in the capillaries, a part of the force with which the heart impels the blood is exercised upon the walls of the vessels which it distends. The distension of each artery increases both its length and its diameter; but the elongation is the most considerable. In their elongation, the arteries change their form, the straight ones becoming curved, and those

already curved becoming more so;* but they recover their previous form as well as their diameter when the ventricular contraction ceases, and their elastic walls recoil. The increase of their curves which accompanies the distension of arteries, and the succeeding recoil, may be well seen in the prominent temporal artery of an old person. The elongation of the artery is in such a case quite manifest.

The dilatation or increase of the diameter of the artery is less evident. In several reptiles, it may be seen without aid in the immediate vicinity of the heart (i. vol. iii. p. 216, *note*), and it may be watched, with a simple magnifying glass, in the aorta of the tadpole. Its slight amount in smaller arteries, the difficulty of observing it in opaque parts, and the rapidity with which it takes place, are sufficient to account for its being, in Mammalia, imperceptible to the eye. But in these also experiment has made its occurrence probable. Poiseuille (lxii. t. ix. p. 44) laid bare the common carotid of a living horse for the space of about twelve inches, and passed beneath it a tube of metal open at one side, which he afterwards closed by means of a narrower portion, so as to complete the tube; he then stopped the ends of the tube, and filled the interior around the artery with water, by means of a glass tube which was connected with the metallic tube. At every pulsation, the water rose 70 millimetres† in the glass tube, the diameter of which was 3 millimetres, and fell again the same distance during each interval. The included portion of artery measured in length 180 millimetres, and its capacity equalled 11,440 cubic millimetres; and since at every beat of the heart it underwent an increase of capacity equal to a column of water of 3 millimetres

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* There is, perhaps, an exception to this in the case of the aorta, of which the curve is by some supposed to be diminished when it is elongated; but if this be so, it is because only one end of the arch is immovable; the other end, with the heart, may move forward slightly when the ventricles contract.

† A millimetre equals 0·0393708 of an English inch.

in diameter and 70 millimetres in height, or about 494 cubic millimetres, it follows, that it was enlarged about $\frac{1}{23}$ of its capacity. It is probable, that part of this enlargement was owing to dilatation; and Flourens, in evidence of such dilatation, says he encircled a large artery with a thin elastic metallic ring cleft at one point, and that at the moment of pulsation the cleft part became perceptibly widened.

This dilatation of an artery, and its elongation producing curvature, or increasing its natural curves, are sensible to the finger placed over it, and produce the pulse. The mind cannot distinguish the sensation produced by the dilatation, from that produced by the elongation and curving; that which it perceives most plainly is the curving, or, as it may be called, the locomotion of the artery; the portion that is under the finger slightly shifting its place as it lengthens in pulsation.

Such, it is generally agreed, is the cause of the pulse felt in any artery; it is produced by the elongation and dilatation of the part under the finger, when it receives its portion of the fresh quantity of blood just discharged from the left ventricle into the aorta and its branches. But some doubt still exists, in reference to the manner in which the pulse is propagated from one part of the arterial system to another. According to the theory of the pulse advanced by E. H. Weber (lxvi.), and adopted by Müller, the impulse given to the blood by the heart distends first merely the arteries nearest to the heart. These, by their elasticity, again contract, and thus cause the distension of the next portion of the arterial system, which, also, in its turn, by contracting, forces the blood into the next portions, and so on; so that a certain interval of time, although a very short one, elapses before this undulation, resulting from the successive compressions of the blood and the dilatation and contraction of the arteries, reaches the most distant parts of the system. In this view the arterial pulse is regarded as the effect of an oscillation or undulation, produced first by the pressure on the blood

in the aorta by the contracting left ventricle, and thence propagated along the walls of the arteries, and along the blood itself.

But against this theory, a very forcible objection presents itself, in the fact pointed out by Mr. F. H. Colt (lxxi. vol. xxxvi. p. 456), that the pulse is perceived in every part of the arterial system previous to the occurrence of the second sound of the heart, that is, previous to the closure of the aortic valves. Now, if the pulse were the effect of a wave propagated by the alternate dilatation and contraction of successive portions of the arterial tube, it ought, in all the arteries, except those "nearest to the heart" to follow, or coincide with, but could never precede, the second sound of the heart; for the first effect of the elastic recoil of the arteries first dilated (which recoil, on Weber's theory, causes the dilatation and pulse in the arteries following those nearest to the heart), is the closure of the aortic valves; and their closure produces the second sound. It appears impossible to reconcile Weber's theory with this fact; the contraction of the arteries nearest to the heart, which he supposes to produce the pulse in those further on, certainly produces, by closing the valves, the second sound of the heart; yet, this sound always, or nearly always, — the exceptions being instances of disease, as in the cases mentioned by Dr. Carpenter (ccvii. p. 241, note), — follows the pulse even in the most distant arteries in which it can be felt. It seems certain, therefore, that the contraction of the arteries nearest the heart does not take place till after the pulse in the more distant ones.

The theory proposed by Mr. Colt, which seems to reconcile all the facts of the case, and especially those two which appear most opposed, namely, that the pulse always precedes the second sound of the heart, and yet is later in the arteries far from the heart than in those near it, may be thus stated:—It supposes that the blood which is impelled onwards by the left ventricle does not so impart its pressure to that which the arteries already

contain, as to dilate the whole arterial system at once; but that as it enters the arteries, it displaces and propels that which they before contained, and flows on with what may be called a *head-wave*, like that which is formed when a rapid stream of water overtakes another moving more slowly. The slower stream offers resistance to the more rapid one, till their velocities are equalized: and, because of such resistance, some of the force of the more rapid stream of blood just expelled from the ventricle, is diverted laterally, and with the rising of the wave the arteries nearest the heart are dilated and elongated. They do not at once recoil, but continue to be distended so long as blood is entering them from the ventricle. The wave at the head of the more rapid stream of blood runs on, propelled and maintained in its velocity by the continuous contraction of the ventricle: and it thus dilates in succession every portion of the arterial system, and produces the pulse in all. The rate of its movement, which represents also the velocity of the blood in the arteries during the ventricular contraction, may be estimated by the interval between the pulse near and far from the heart. At length, the whole arterial system (wherein a pulse can be felt) is dilated; and at this time, when the wave we have supposed has reached all the smaller arteries, the entire system may be said to be simultaneously dilated; then it begins to contract, and the contractions of its several parts ensue in the same succession as the dilatations, commencing at the heart. The contraction of the first portion produces the closure of the valves and the second sound of the heart; and both it and the progressive contractions of all the more distant parts maintain, as already said, that pressure on the blood during the inaction of the ventricle, by which the stream of the arterial blood is sustained between the jets, and is finally equalized by the time it reaches the capillaries.

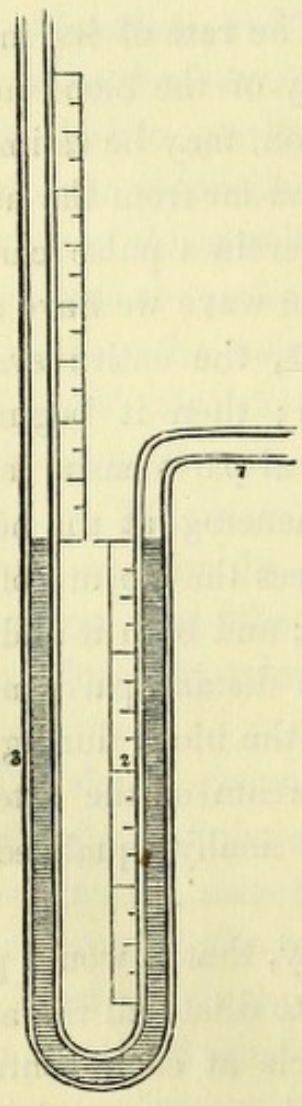
It may seem an objection to this theory, that it would probably require a larger quantity of blood to dilate all the arteries than can be discharged by the ventricle at each contraction. But the quantity necessary for such a purpose is less

than might be supposed. Injections of the arteries, prove that, including all down to those of about one-eighth of a line in diameter, they do not contain, on an average, more than one and a half pints of fluid, even when distended. There can be no doubt, therefore, that the three ounces which the ventricle is supposed to discharge at each contraction, being added to that which already fills the arteries, would be sufficient to distend them all.

### *Force of the Blood in the Arteries.*

The force with which the ventricles act in their contraction, and the reasons for believing it sufficient for the circulation of the blood, have been already mentioned. Both calculation and experiment have proved, that very little of this force is consumed in the arteries. Dr. Thomas Young (xliii. vol. xcix.) calculated that the loss of force in overcoming friction ando ther hindrances in the arteries would be so slight, that if one tube were introduced into the aorta, and another into any other artery, even into one as fine as hair, the blood would rise in the tube from the small vessel to within two inches of the height to which it would rise from the large vessel. The correctness of the calculation is established by the experiments of Poiseuille (lxii. t. viii. p. 272). who invented an instrument named a hæmadynamometer, for estimating the statical pressure exercised by the blood upon the walls of the arteries. It consists of a long glass tube, bent so as to have a short horizontal portion (fig. 11, 1), a branch (2) descending at right angles from it, and a long ascending branch (3). Mercury poured into the ascending

*Fig.* 11.



and descending portions, will necessarily have the same level in both branches, and in a vertical position the height of its column must be the same in both. If, now, the blood is made to flow from an artery, through the horizontal portion of the tube (which should contain a solution of carbonate of potash to prevent coagulation) into the descending branch, it will exert on the mercury a pressure equal to the force by which it is moved in the arteries; and the mercury will, in consequence, descend in this branch, and ascend in the other. The depth to which it sinks in the one branch, added to the height to which it rises in the other, will give the whole height of the column of mercury which balances the pressure exerted by the blood; the weight of the blood which takes the place of the mercury in the descending branch, and which is more than ten times less than the same quantity of quicksilver, being substracted. Poiseuille thus calculated the force with which the blood moves in an artery, according to the laws of hydrostatics, from the diameter of the artery, and the height of the column of quicksilver; that is to say, from the weight of a column of mercury, whose base is a circle of the same diameter as the artery, and whose height is equal to the difference in the levels of the mercury in the two branches of the instrument. He found the blood's pressure equal in all the arteries examined; difference in size, and distance from the heart, being unattended by any corresponding difference of force in the circulation. The height of the column of mercury displaced by the blood, was the same in all the arteries of the same animal.

From the mean result of several observations on horses and dogs, he calculated that the force with which the blood is moved in any large artery, is capable of supporting a column of mercury, six inches and one and a-half lines in height, or a column of water seven feet one line in height. With these results, the more recent observations of Valentin (iv. p. 441), Spengler (lxxx. 1844), and Ludwig (lxxx. 1847, p. 242), closely accord. Poiseuille's experiments having thus shown to him that the

force of the blood's motion is the same in the most different arteries, he concluded that, to measure the amount of the blood's pressure in any artery of which the calibre is known, it is necessary merely to multiply the area of a transverse section of a vessel by the height of the column of mercury which is already known to be supported by the force of the blood in any part of the arterial system. The weight of a column of mercury of the dimensions thus found, will represent the pressure exerted by the column of blood. And assuming that the mean of the greatest and least height of the column of mercury found by experiments on different animals, to be supported by the force of the blood in them, is equivalent to the height of the column which the force of the blood in the human aorta would support, he calculated that about 4 lbs. 4 oz. avoirdupois, would indicate the static force with which the blood is impelled into the human aorta. By the same calculation, he estimated the force of the circulation in the aorta of the mare to be about 11 lbs. 9 oz. avoirdupois: and that in the radial artery at the human wrist only 4 drs. We have already seen that the muscular force of the right ventricle is equal to only half that of the left, consequently, if Poiseuille's estimate of the latter be correct, the force with which the blood is propelled into the lungs will only be equal to 2 lbs. 2 oz. avoirdupois.

The amounts above stated indicate the pressure exerted by the blood at the several parts of the arterial system at the time of the ventricular contraction. During the dilatation, this pressure is somewhat diminished. Hales observed, that the column of blood in the tube inserted into an artery, falls an inch, or rather more, after each pulse; Ludwig (lxxx. 1847, p. 242) has observed the same, and recorded it more minutely. The pressure is also influenced by the various circumstances which affect the action of the heart; the diminution or increase of the pressure being proportioned to the weaker or stronger action of this organ. Valentin observed that, on increasing the amount of blood by the injection of a fresh quantity into it,

the pressure in the vessels was also increased, while a contrary effect ensued on diminishing the quantity of blood.

Poiseuille, Ludwig, and others have confirmed what Haller and Magendie observed, namely, that the strength of the blood's impulse in the arteries is increased during expiration; in which act the chest is contracted, and the large vessels in consequence compressed. The column of mercury in the hæmadynamometer rises somewhat at each expiration, and falls during inspiration. The extent of the rise and fall of the mercury observed by Poiseuille, was the same in arteries, the distance of which from the heart was different; and in ordinary tranquil respiration amounted to from four to ten lines. The decrease of the arterial blood's impulse in inspiration is in some persons so great, that the pulse at the radial artery becomes imperceptible when inspiration is long continued and the breath held; its increase in expiration is well shown in the increased pain and throbbing of an inflamed part during coughing, and in the frequency of rupture in diseased arteries during violent expiratory efforts. These things will be again referred to in speaking of the movement of the venous blood.

## THE CAPILLARIES.

In all organic textures, except the corpora cavernosa of the penis, and the uterine placenta, the transmission of the blood from the minute branches of the arteries to the minute veins is effected through a network of microscopic vessels, in the meshes of which the proper substance of the tissue lies (fig. 12). This may be seen in all minutely injected preparations; and during life, by the aid of the microscope, in any transparent parts,—such as the web of the frog's foot, the lungs, tongue, and the urinary bladder of the frog, the tail or external branchiæ of the tadpole, the incubated egg, young fishes, the wings of the bat, and the mesentery of all Vertebrata,—and even in some opaque textures of the larva of the salamander by means of a simple microscope. The ramifications of

*Fig.* 12.*

the minute arteries form repeated anastomoses with each other and give off the capillaries which, by their anastomoses, compose a continuous and uniform network, from which the venous radicles, on the other hand, take their rise. The reticulated vessels connecting the arteries and veins are called capillary, on account of their minute size; and intermediate vessels on account of their position. The point at which the arteries terminate and the minute veins commence, cannot be exactly defined, for the transition is gradual; but the intermediate network has, nevertheless, this peculiarity, that the small vessels which compose it maintain the same diameter throughout: they do not diminish in diameter in one direction, like arteries and veins; and the meshes of the network that they compose are more uniform in shape and size than are those formed by the anastomoses of the minute arteries and veins.

The *diameter* of the capillary vessels varies somewhat in the different textures of the body, the most common size being about $\frac{1}{3000}$th of an inch. Among the smallest may be mentioned those of the brain, and of the follicles of the mucous membrane of the intestines; among the largest, those of the skin, and especially those of the medulla of bones.

The *form of the capillary network* presents considerable variety in the different textures of the body: the varieties consisting principally of modifications of two chief kinds of mesh, the rounded and the elongated. That kind in which the meshes

* Fig. 12. Blood-vessels of an intestinal villus, representing the arrangement of capillaries between the ultimate venous and arterial branches; *a*, *a*, the arteries; *b*, the vein.

or interspaces have a roundish form is the most common, and prevails in those parts in which the capillary network is most dense, such as the lungs, most glands, and mucous membranes and the cutis. The meshes of this kind of network are not quite circular, but more or less angular, sometimes presenting a nearly regular quadrangular or polygonal form, but being more frequently irregular. The capillary network with elongated meshes is observed in parts in which the vessels are arranged among bundles of fine tubes or fibres, as in muscles and nerves. In such parts, the meshes usually have the form of a parallelogram, the short sides of which may be from three to eight or ten times less than the long ones; the long sides always corresponding to the axis of the fibre or tube, by which it is placed. The appearance of both the rounded and elongated meshes is much varied according as the vessels composing them have a straight or tortuous form. Sometimes the capillaries have a looped arrangement, a single capillary projecting from the common network into some prominent organ, and returning after forming one or more loops, as in the papillæ of the tongue and skin. Whatever be the form of the capillary network in any tissue or organ, it is, as a rule, found to prevail in the corresponding parts of all animals.

The *number* of the capillaries and the *size of the meshes* in different parts determine in general the degree of *vascularity* of those parts.—The parts in which the network of capillaries is closest, that is, in which the meshes or interspaces are the smallest, are the lungs and the choroid membrane of the eye. In the iris and ciliary body, the interspaces are somewhat wider, yet very small. In the human liver, the interspaces are of the same size, or even smaller than the capillary vessels themselves. In the human lung they are smaller than the vessels. In the human kidney, and in the kidney of the dog, the diameter of the injected capillaries, compared with that of the interspaces, is in the proportion of one to four, or of one to three. The brain receives a very large quantity of blood; but the capillaries in which the blood is distributed through its sub-

stance are very minute, and less numerous than in some other parts. Their diameter, according to E. H. Weber, compared with the long diameter of the meshes, being in proportion of one to eight or ten; compared with the transverse diameter, in the proportion of one to four or six. In the mucous membranes—for example, in the conjunctiva—and in the cutis vera, the capillary vessels are much larger than in the brain, and the interspaces narrower,—namely, not more than three or four times wider than the vessels. In the periosteum the meshes are much larger. In the cellular coat of arteries, the width of the meshes is ten times that of the vessels (Henle).

It may be held as a general rule, that the more active the functions of an organ are, the more vascular it is; that is, the closer is its capillary network and the larger its supply of blood. Hence the narrowness of the interspaces in all glandular organs, in mucous membranes, and in growing parts; their much greater width in bones, ligaments, and other very tough and comparatively inactive tissues; and the complete absence of vessels in cartilages, the dense tendons of adults, and such parts, in which, probably, very little organic change occurs after they are once formed. But the general rule must be modified by the consideration, that some organs, such as the brain, though they have small and not closely arranged capillaries, may receive large supplies of blood by reason of its more rapid movement. When an organ has large arterial trunks and a comparatively small supply of capillaries, the movement of the blood through it will be so quick, that it may, in a given time, receive as much fresh blood as a more vascular part with smaller trunks, though at any given instant the less vascular part will have in it a smaller quantity of blood.

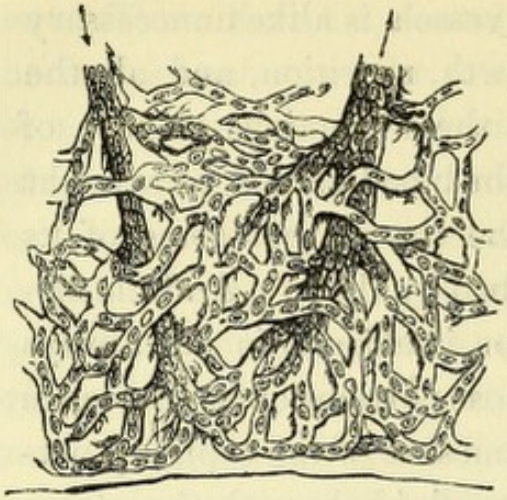
Microscopic observations and minute injections have shewn that the capillary vessels are merely the fine tubes which form the medium of transition from arteries to veins, and that no other kind of vessel arises from them; that the minute arteries have no other mode of termination than the communication with the veins by means of the capillaries; in a word, that there are no

exhalant or other vessels terminating by open extremities. The hypothesis of the existence of such vessels is alike unnecessary to the explanation of secretion, growth, nutrition, and all the other functions of a part. All that these functions require of the vessels is, that for each tissue, the blood should be brought so near to the active elements of the tissue, that some of its fluid part may be absorbed or imbibed by them. And the distance through which such imbibition is effected is not always small; in the brain, for example, those portions of its substance which lie in the middle of the wide meshes of the capillary network must be nourished by imbibing fluid through the spaces between them and the nearest vessels; so also in bone, where the vessels are yet wider apart. But the instances in which such imbibition is effected through the greatest distance are in what are called non-vascular tissues, which receive no blood-vessels into their own substance, and are nourished by the fluid absorbed from the vessels of the adjacent vascular parts; as the cornea from the vessels of the conjunctiva, the lens from those of the posterior layer of its capsule, and the articular cartilage from the vessels of the subjacent bone. The difference of nutrition in vascular and non-vascular tissues is only one of degree; in all parts alike the elementary structures are outside the vessels and obtain new materials from the blood by imbibition; but the imbibition has to be accomplished through a greater distance in the less than in the more vascular parts.

The *structure* of the capillaries offers little hindrance to such imbibition. Their walls are composed of exceedingly fine, transparent, and apparently homogeneous membrane, in which are imbedded, here and there, minute oval corpuscles, probably the persistent nuclei of the cells from which the vessels were originally formed. Only in the largest capillaries are there traces of an epithelial lining like that of the arteries, or of filaments, like rudiments of a circularly-fibrous coat.

*In the Circulation in the Capillaries*, as seen in any transparent part of a living adult animal by means of the microscope

*Fig.* 13.*



(fig. 13), the blood flows with a constant equable motion. In very young animals, the motion, though continuous, is accelerated at intervals corresponding to the pulse in the larger arteries, and a similar motion of the blood is also seen in the capillaries of adult animals when they are feeble: if their exhaustion is so great that the power of the heart is still more diminished, the red corpuscles are observed to have merely the periodic motion, and to remain stationary in the intervals; while, if the debility of the animal is extreme, they even recede somewhat after each impulse, apparently because of the elasticity of the capillaries and the tissues round them. These observations may be added to those already (p. 100) advanced to prove, that, even in the state of great debility, the action of the heart is sufficient to impel the blood through the capillary vessels. Moreover, Dr. Marshall Hall (xciv. 1843) having placed the pectoral fin of an eel in the field of the microscope and compressed it by the weight of a heavy probe, observed that the movement of the blood in the capillaries became obviously pulsatory, the pulsations being synchronous with the contractions of the ventricle. This power of the heart to propel the blood through a second set of capillaries affords an explanation of the fœtal circulation, and of the more difficult problem, the circulation through the acardiac fœtus. The pulsatory motion of the blood in the capillaries cannot be attributed to an action in these vessels; for, when the animal is tranquil, they present not the slightest change in their diameter.

It is in the capillaries, that the chief resistance is offered to the progress of the blood; for in them the friction of the blood

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* Fig. 13. Capillaries in the web of the frog's foot magnified.

is greatly increased by the enormous multiplication of the surfaces with which it is brought in contact. The velocity of the blood is, also, in them reduced to its minimum, because of the widening of the stream. If, as Professor Müller says, the sectional area of all the branches of a vessel united were always the same as that of the vessel from which they arise, and if the aggregate sectional area of the capillary vessels were equal to that of the aorta, the mean rapidity of the blood's motion in the capillaries would be the same as in the aorta and largest arteries; and, if a similar correspondence of capacity existed in the veins and arteries, there would be an equal correspondence in the rapidity of the circulation in them. It is quite true, that the force with which the blood is propelled in the arteries, as shewn by the quantity of blood which escapes from them in a certain space of time, is much greater than that with which it moves in the veins; but this force has to overcome all the resistance offered in the arterial and capillary system—the heart itself, indeed, must overcome this resistance; so that the excess of the force of the blood's motion in the arteries is expended in overcoming this resistance, and the rapidity of the circulation in the arteries, even from the commencement of the aorta, would be the same as in the veins and capillaries, if the aggregate capacity of each of the three systems of vessels were the same.

But since the aggregate sectional area of the branches is greater than that of the trunk from which they arise, the rapidity of the blood's motion will necessarily be greater in the trunk, and will diminish in proportion as the aggregate capacity of the vessels increases during their ramification: in the same manner as, other things being equal, the velocity of a stream diminishes as it widens.

The observations of Hales (lxvii. vol. ii.), E. H. Weber (lxxx. 1838, p. 450), and Valentin (iv. vol. i. p. 468), agree very closely as to the rate of the blood in the capillaries of the frog: and the mean of their estimates gives the velocity of the systemic capillary circulation at about one inch per minute.

Through the pulmonic capillaries, the rate of motion, according to Hales, is about five times that through the systemic ones. The velocity in the capillaries of warm-blooded animals is greater, but has not yet been accurately estimated. If it be assumed to be three times as great as in the frog, still the estimate may seem too low, and inconsistent with the facts which shew that the whole circulation is accomplished in about a minute. But the whole length of capillary vessels, through which any given portion of blood has to pass, probably does not exceed $\frac{1}{30}$ of an inch; and therefore the time required for each quantity of blood to traverse its own appointed portion of the general capillary system will scarcely amount to a second: while in the pulmonic capillary system the length of time required will be much less even than this.

The estimates given above are drawn from observations of the movements of the red blood-corpuscles, which move in the centre of the stream. At the circumference of the stream, in contact with the walls of the vessels, and adhering to them, there is a layer of liquor sanguinis which appears to be motionless. The existence of this *still layer*, as it is termed, is inferred, both from the general fact that such an one exists in all fine tubes traversed by fluid, and from what can be seen in watching the movements of the blood-corpuscles. The red corpuscles occupy the middle of the stream, and move with comparative rapidity; the colourless lymph-corpuscles run much more slowly by the walls of the vessel; while next to the wall there is often a transparent space in which the fluid appears to be at rest; for if any of the corpuscles happen to be forced within it, they move more slowly than before, rolling lazily along the side of the vessel, and often adhering to its wall. Part of this slow movement of the pale corpuscles, and their occasional stoppage may be due, as E. H. Weber has suggested, to their having a natural tendency to adhere to the walls of the vessels. Sometimes, indeed, when the motion of the blood is not strong, many of the white corpuscles collect

in a capillary vessel, and for a time entirely prevent the passage of the red corpuscles. But there is no doubt that such a still layer of liquor sanguinis exists next the walls of the vessels, and it is between it and the tissues around the vessels that those interchanges of particles take place which ensue in nutrition, secretion, and absorption by the blood vessels; interchanges which are probably facilitated by the tranquillity of the fluids between which they are effected.

There is no reason for supposing that either the pale or red corpuscles ever remain permanently fixed to the wall of the vessels, and become united with them, or that they pass through the walls to enter into the structure of the tissues. Their office appears to be fulfilled exclusively within the vessels.

Much diversity of opinion has long prevailed respecting the possession by capillaries of any power to aid the progressive motion of the blood. It may be stated, with tolerable certainty, that the capillaries themselves possess no such power, and that the influence which they seem to exercise on the movement of their contained blood, is referable in part to the action of the small arteries, and in part to the results of the relation which exists between the tissues without, and the blood within, the capillaries.

Thus, the capillaries contract on the application of cold: but this may be due not to any contraction similar to that of muscular tissue, but to their elasticity, and that of the surrounding tissues which close in, when, by the contraction of the small arteries (which, as already stated, can be made to contract by cold), the flow of blood into the capillaries is diminished.

The apparent contraction of the capillaries, too, on the application of certain irritating substances, and during fear, and their dilatation in blushing, may be similarly referred to the action of the small arteries, rather than to that of the capillaries themselves.

Still it is very probable that some influence in aid of the general circulation takes place in the capillary system.

The results of morbid action, as well as the phenomena of health, strongly support such a view. For example, when the access of oxygen to the lungs is prevented, the circulation through the pulmonic capillaries is gradually retarded, the blood-corpuscles cluster together, and their movement is eventually almost arrested, even while the action of the heart continues. In inflammation, also, the capillaries of an inflamed part are enlarged and distended with blood, which either moves very slowly, or is completely at rest. In both these cases the phenomena are local, and independent of the action of the heart, and appear to result from some alteration in the blood, which increases the adhesion of its particles to one another, and to the walls of the capillaries, to an amount which the propelling action of the heart is not able to overcome.

The temporary increase in the size of the capillaries, and in the quantity of blood moving through them in any part, during an unusually active discharge of its functions, has been cited as evidence of their exercising some power to determine the amount of blood that shall traverse them. Instances of such enlargement are seen in the turgescence of an actively secreting or quickly growing part. But the control here displayed, may be exercised, not by the capillaries themselves, but by that relation, whatever be its nature, which exists between every tissue and the blood, and by which the condition of the tissue determines the quantity of blood to be supplied to it; as, in the rudimental state, the condition of each organ or tissue determines the first formation and supply of blood to it.

It may be concluded, then, that the capillaries, which are formed of a simple homogeneous membrane, destitute of all contractile power apart from elasticity, can of themselves exercise no direct influence on the movement of their contents: yet that the constant interchange of relations between the blood and the tissues outside the vessels does in some measure facilitate the movement of blood through the capillary

system, and thus constitute one of the assistant forces of the circulation.*

### *The Veins.*

In *structure* the coats of veins bear a general resemblance to those of arteries. They possess, however, no complete elastic coat; what elastic tissue they have, is interwoven in their fibro-cellular tissue, which, being itself also extensile and elastic, enables them to recover from the temporary extensions to which they are liable. That part of their walls also which corresponds with the muscular coat of the arteries, is composed of fibres resembling those of fibro-cellular tissue; combined with these, however, are well-marked fibre-cells of organic muscle, through the agency of which the veins probably possess some power of independently contracting on their contents. To the great trunks of the veins, where they are near the auricles, more of this power is given by a circular layer of striated muscular fibres, like those of the auricles, which takes the place of the organic muscular and fibro-cellular tissue, and the action of which has been already referred to (p. 77). But in the rest of the veins, the contractile power is probably weak and of slow action; sufficient, however, to enable them to adapt themselves to the size required when they receive less than their average supply of blood through the arteries; while to the usual, or more than the usual supply, they are adapted by the extensile and elastic property of all their coats.

The chief influence that the veins have in the circulation, is effected with the help of the *valves*, which are placed in all veins that are subject to local pressure from the muscles between or near which they run. The general construction of

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* For a clever and elaborate essay on the subject, consult the British and Foreign Medico-Chirurgical Review, vol. xv. p. 372, wherein Mr. Savory brings together the principal arguments in favour of a "capillary circulation," and meets the objections to them.

these valves is similar to that of the semilunar valves of the aorta and pulmonary artery, already described (p. 80); but their free margins are turned in the opposite direction, *i.e. towards* the heart, so as to stop any movement of blood backward in the veins. They are commonly placed in pairs, at various distances in different veins, but almost uniformly in each. In the smaller veins, single valves are often met with; and three or four are sometimes placed together, or near one another, in the largest veins, such as the subclavian, and at their junction with the jugular veins. The valves are semilunar; the unattached edge being in some examples concave, in others straight. They are composed of inextensile fibrous tissue, and are covered with epithelium like that lining the veins. During the period of their inaction, when the venous blood is flowing in its proper direction, they lie by the sides of the veins; but when in action, they close together like the valves of the arteries, and offer a complete barrier to any backward movement of the blood.

The principal obstacle to the circulation is already overcome when the blood has traversed the capillaries; and the force of the heart which is not yet consumed is sufficient to complete its passage through the veins, in which the obstructions to its movement are very slight. For the formidable obstacle supposed to be presented by the gravitation of the blood, has no real existence, since the pressure exercised by the column of blood in the arteries, will be always sufficient to support a column of venous blood of the same height as itself: the two columns mutually balancing each other. Indeed, so long as both arteries and veins contain continuous columns of blood, the force of gravitation, whatever be the position of the body, can have no power to move or resist the motion of any part of the blood in any direction: as if one had a circular tube full of fluid at every part, the fluid might be made to circulate with equal facility in either direction, or in any position of the tube. The lowest blood-vessels have, of course, to bear the greatest amount of pressure; the pressure on each part being directly

proportionate to the height of the column of blood above it: hence their liability to distension. But this pressure bears equally on both arteries and veins, and cannot either move, or resist the motion of, the fluid they contain, so long as the columns of fluid are of equal height in both and continuous. Their condition may, in this respect, be compared with that of a double bent tube full of fluid held vertically; whatever be the height and gravitation of the columns of fluid, neither of them can move of its own weight, each being supported by the other; yet the least pressure on the top of either column will lift up the other: so, when the body is erect, the least pressure on the column of arterial blood may lift up the venous blood, and, were it not for the valves, the least pressure on the venous might lift up the arterial column.

In experiments to determine what proportion of the force of the left ventricle remains to propel the blood in the veins Valentin found that the pressure of the blood in the jugular vein of a dog, as estimated by the hæmadynamometer, did not amount to more than $\frac{1}{11}$ or $\frac{1}{12}$ of that in the carotid artery of the same animal; and this estimate is confirmed, in the instances of several other arteries and their corresponding veins, by Mogk (xxxiii. 1845, p. 33). In the upper part of the inferior vena cava, Valentin could scarcely detect the existence of any pressure, nearly the whole force received from the heart having been, apparently, consumed during the passage of the blood through the capillaries (iv. p. 477). But, slight as this remanent force might be (and the experiment in which it was estimated would reduce the force of the heart below its natural standard), it would be enough to complete the circulation of the blood; for, as already stated (p. 94), the spontaneous dilatation of the auricles and ventricles, though it may not be forcible enough to assist the movement of blood into them, is adapted to offer to that movement no obstacle.

Some assistance is given to the venous circulation by the *respiratory movements* of the chest; and some, occasionally, but

very effectually, by the *actions of the muscles* capable of pressing on such veins as have valves.

The *effect of muscular pressure* on such veins may be thus explained. When pressure is applied to any part of a vein, and the current of blood in it is obstructed, the portion behind the seat of pressure becomes swollen and distended as far back as to the next pair of valves. These, acting like the arterial valves, and being, like them, inextensile both in themselves and at their margins of attachment, do not follow the vein in its distension, but are drawn out towards the axis of the canal. Then, if the pressure continues on the vein, the compressed blood, tending to move equally in all directions, presses the valves down into contact at their free edges, and they close the vein and prevent regurgitation of the blood. Thus, whatever force is exercised by the pressure of the muscles on the veins, is distributed partly in pressing the blood onwards in the proper course of the circulation, and partly in pressing it backwards and closing the valves behind.

The circulation might lose as much as it gains by such compression of the veins, if it were not for the numerous anastomoses by which they communicate with one another; for through these, the closing up of the venous channel by the backward pressure is prevented from being any serious hindrance to the circulation, since the blood, of which the onward course is arrested by the closed valves, can at once pass through some anastomosing channel, and proceed on its way by another vein. Thus, therefore, the effect of muscular pressure upon veins that have valves, is turned almost entirely to the advantage of the circulation; the pressure of the blood onwards is all advantageous, and the pressure of the blood backwards is prevented from being a hindrance by the closure of the valves and the anastomoses of the veins.

The effects of such muscular pressure are well shown by the acceleration of the stream of blood when, in venesection, the muscles of the fore-arm are put in action, and by the general acceleration of the circulation during active exercise; and the

numerous movements which are continually taking place in the body while awake, though their single effects may be less striking, must be an important auxiliary to the venous circulation. Yet they are not essential; for the venous circulation continues unimpaired in parts at rest, in paralysed limbs, and in parts in which the veins are not subject to any muscular pressure.

Besides the assistance thus afforded by muscular pressure to the movement of blood along veins possessed of valves, it has been discovered by Mr. Wharton Jones (xliii. 1852), that in some instances at least, the coats of veins furnished with valves possess the remarkable property of rhythmical contraction and dilatation, whereby the current of blood within them is distinctly accelerated. Mr. Jones observed this phenomenon repeatedly in the veins of bats' wings, and found that the contraction occurred, on an average, about ten times in the minute; the existence of valves preventing regurgitation, the entire effect of the contractions was auxiliary to the onward current of blood. It is reasonable to infer that veins in other parts may, when furnished with valves, possess a like power; Schiff, indeed, has proved its existence in the veins of the rabbit's ear.

The *respiratory movements* of the chest also assist the circulation of the blood in the systemic veins: at least, the more forcible respiratory movements do; the ordinary ones are too weak to produce any considerable effect. The effect of expiration in increasing the pressure of the blood in the arteries has been already mentioned (page 119), and is minutely illustrated by the experiments of Ludwig (lxxx. 1847, p. 242). It acts as the pressure of contracting muscles does upon the veins, and is advantageous to the movement of arterial blood while the aortic valves are closed, because during this time the backward pressure cannot wholly neutralise the benefit of the pressure forwards. The increased pressure on the blood in the arteries during expiration is also propagated through the capillaries to some of the veins; for Magendie has shewn

that the stream of venous blood from the lower end of a divided vein becomes stronger during each expiration.

But on the whole, little advantage is derived to the circulation from the movements of expiration, since the same pressure which drives on the arterial blood with increased force must, in some degree, retard the blood in the veins, and obstruct its passage to the heart. The effect of such retardation is shewn in the swelling-up of the veins of the head and neck, and the lividity of the face, during coughing, straining, and similar violent expiratory efforts. The effects shewn in these instances are due both to some regurgitation of blood in the great veins, and to the accumulation of blood in the veins of the head and face, which are constantly more and more filled by the influx from the arteries, and are not able to empty themselves into the vena cava superior. The regurgitation, however, is stopped, or much diminished, by the valves at the junction of the jugular and subclavian veins, by which also the disadvantageous effects of the forced expirations are limited.

The act of inspiration is favourable to the venous circulation, and its effect is not quite counterbalanced by its tending to draw the arterial, as well as the venous, blood towards the cavity of the chest. When the chest is enlarged in inspiration, the additional space within it is filled chiefly by the fresh quantity of air which passes through the trachea and bronchial passages to the vesicular structure of the lungs. But the blood being, like the air, subject to the atmospheric pressure, some of it, also, is at the same time pressed towards the expanding cavity of the chest, and therein towards the heart. The effect of this in the arterial current is hindered by the aortic valves, while they are closed; and is less than it is on the venous current in the same proportion as the orifice of the aorta is less than the united orifices of the two venæ cavæ.

Sir David Barry was the first who shewed plainly this effect of inspiration on the venous circulation, and mentions the fol-

lowing experiment in proof of it. He introduced one end of a bent glass tube into the jugular vein of an animal, the vein being tied above the point where the tube was inserted; the inferior end of the tube was immersed in some coloured fluid. He then observed that at the time of each inspiration the fluid ascended in the tube, while during expiration it either remained stationary, or even sank. Poiseuille confirmed the truth of this observation, in a more accurate manner, by means of his hæmadynamometer. And a like confirmation has been since furnished by Valentin (iv. p. 478), and in minute details by Ludwig (lxxx. 1847, p. 242).

The effect of inspiration on the veins is observable only in the large ones near the thorax. Poiseuille could not detect it by means of his instrument in veins more distant from the heart,—for example, in the veins of the extremities. And its beneficial effect would be neutralised were it not for the valves; for he found that, when he repeated Sir D. Barry's experiments, and passed the tube so far along the veins that it went beyond the valves nearest to the heart, as much fluid was forced back into the tube in every expiration as was drawn in through it in every inspiration.

On the whole, therefore, the respiratory movements of the chest are advantageous to the systemic circulation. On the pulmonary circulation they appear to produce little effect, but that little, according to Donders (xxxiii. 1853, p. 287, e. s.), is advantageous. The additional force which expiration gives to the arterial current is not counterbalanced by the retardation of the venous current, because, the valves of the veins closing, limit the regurgitation from the chest; and though the blood behind or above these valves is retarded while they are close, yet it goes on with accumulated force as soon as they are open again. On the other hand, the retardation of the arterial blood by the act of inspiration is less than the acceleration of the venous blood, because the orifice of the aorta is less than that of the venæ cavæ.

The disturbance which hurried respiration and struggling

produce in the movement of the venous blood makes it exceedingly difficult to determine the average force or velocity of the venous stream. The *velocity* of the blood is greater in the veins than in the capillaries, but less than in the arteries : and to this are adapted the relative capacities of the arterial and venous systems ; for since the veins must return to the heart all the blood that they receive from it in a given time, through the arteries, their larger size and proportionally greater number must compensate for the slower movement of the blood through them. If an accurate estimate of the proportionate areas of arteries and the veins corresponding to them could be made, we might, from the velocity of the arterial current calculate that of the venous. Perhaps a fair approximation to such an estimate is, that the capacity of the veins is about three times as great as that of the arterial system ; and that the velocity of the blood's motion is about one-third less in the former than in the latter. And this is not a slow movement; for if we stop the circulation at the beginning of any superficial vein, and empty the upper part of the vein, immediately upon removing the finger the blood will move along the vein faster than the eye can follow it. The rate at which the blood moves in the veins gradually increases the nearer it approaches the heart, for the sectional area of the venous trunks, compared with that of the branches opening into them, becomes gradually less as the trunks advance towards the heart.

Having now considered the share which each of the circulatory organs has in the propulsion and direction of the blood, we may speak of their combined effects, especially in regard to the velocity with which the movement of the blood through the whole round of the circulation is accomplished. As Müller says, the rate of the blood's motion in the vessels must not be judged of by the rapidity with which it flows from a vessel when divided. In the latter case, the rate of motion is the result of the entire pressure to which the whole mass of blood is subjected in the vascular system, and which at the point of the incision in the vessel meets with no resistance. In the closed

vessels, on the contrary, no portion of blood can be moved forwards but by impelling on the whole mass, and by overcoming the resistance arising from friction in the smaller vessels.

From the rate at which the blood escapes from opened vessels we could only judge, in general, that its velocity is, as already said, greater in arteries than in veins, and in both than in the capillaries. More satisfactory data for the estimates are afforded by the results of experiments to ascertain the rapidity with which poisons introduced into the blood are transmitted from one part of the vascular system to another. From eighteen such experiments on horses, Hering deduced that the time required for the passage of a solution of ferrocyanide of potassium, mixed with the blood, from one jugular vein (through the right side of the heart, the pulmonary circulation, the left cavities of the heart, and the general circulation) to the jugular vein of the opposite side, varies from twenty to thirty seconds. The same substance was transmitted from the jugular vein to the great saphena in twenty seconds; from the jugular vein to the masseteric artery, in between fifteen and thirty seconds; to the facial artery in one experiment, in between ten and fifteen seconds; in another experiment, in between twenty and twenty-five seconds: in its transit from the jugular vein to the metatarsal artery, it occupied between twenty and thirty seconds, and in one instance more than forty seconds. The result was nearly the same whatever was the rate of the heart's action.

Poiseuille's observations (xxxi. 1843) accord completely with the above; and shew, moreover, that when the ferrocyanide is injected into the blood with other substances, such as acetate of ammonia, or nitrate of potash (solutions of which, as other experiments have shewn, pass quickly through capillary tubes), the passage from one jugular vein to the other is effected in from eighteen to twenty-four seconds; while, if instead of these, alcohol is added, the passage is not completed until from forty to forty-five seconds after injection. Still greater rapidity of transit has been observed by Mr. J. Blake (xciv. Oct. 1841), who found that nitrate of baryta injected into the jugular vein

of a horse could be detected in blood drawn from the carotid artery of the opposite side in from fifteen to twenty seconds after the injection. In sixteen seconds a solution of nitrate of potash, injected into the jugular vein of a horse, caused complete arrest of the heart's action, by entering and diffusing itself through the coronary arteries. In a dog, the poisonous effects of strychnia on the nervous system were manifested in twelve seconds after injection into the jugular vein; in a fowl, in six and a half seconds, and in a rabbit in four and a half seconds.

In all these experiments, it is assumed that the substance injected moves with the blood, and at the same rate as it, and does not move from one part of the organs of circulation to another by diffusing itself through the blood or tissues more quickly than the blood moves. The assumption is so probable, that it may be considered nearly certain that the times above-mentioned, as occupied in the passage of the injected substances, are those in which the portion of blood into which each was injected was carried from one part to another of the vascular system. It would, therefore, appear that a portion of blood can traverse the entire course of the circulation, in the horse, in half a minute; of course it would require longer to traverse the vessels of the most distant part of the extremities than to go through those of the neck; but taking an average length of vessels to be traversed, and assuming, as we may, that the movement of blood in the human subject is not slower than in the horse, it may be concluded that one minute, which is the estimate usually adopted of the average time in which the blood completes its entire circuit in man, is rather above than below the actual rate.

Another mode of estimating the general velocity of the circulating blood is by calculating it from the quantity of blood supposed to be contained in the body, and from the quantity which can pass through the heart in each of its actions. But the conclusions arrived at by this method are less satisfactory. For the estimates both of the total quantity of blood, and of

the capacity of the cavities of the heart, are as yet only approximated to the truth. Still, the most careful of the estimates thus made accord with those already mentioned; for Valentin has, from these data, calculated that the blood may all pass through the heart in from $43\frac{3}{4}$ to $62\frac{2}{3}$ seconds.

The estimate from the speed at which the blood may be seen moving in transparent parts, is not opposed to this. For, as already stated (p. 125), though the movement through the capillaries may be very slow, yet the length of capillary vessel through which any portion of blood has to pass is very small. Even if we estimate that length at the tenth of an inch, and suppose the velocity of the blood therein to be only one inch per minute, then each portion of blood may traverse its own distance of the capillary system in about six seconds. There would, thus, be plenty of time left for the blood to travel through its circuit in the larger vessels, in which the greatest length of tube that it can have to traverse in the human subject does not exceed ten feet.

All the estimates here given are averages; but of course the time in which a given portion of blood passes from one side of the heart to the other, varies much according to the organ it has to traverse. The blood which circulates from the left ventricle, through the coronary vessels, to the right side of the heart, requires a far shorter time for the completion of its course than the blood which flows from the left side of the heart to the feet, and back again to the right side of the heart; for the circulation from the left to the right cavities of the heart may be represented as forming a number of arches, varying in size, and requiring proportionately various times for the blood to traverse them; the smallest of these arches being formed by the circulation through the coronary vessels of the heart itself. The course of the blood from the right side of the heart, through the lungs, to the left, is shorter than most of the arches described by the systemic circulation, and in it the blood flows, *cæteris paribus*, much quicker than in most of the vessels which belong to the aortic circulation. For although the quantity of blood con-

tained, at any instant, in the greater circulation of the body, is far greater than the quantity within the lesser circulation, yet, in any given space of time, as much blood must pass through the lungs as passes in the same time through the systemic circulation. If the systemic vessels contain five times as much blood as the pulmonary, the blood in them must move five times as slow as in these; else, the right side of the heart would be either overfilled or not filled enough.

### *Peculiarities of the Circulation in different Parts.*

The most remarkable peculiarities attending the circulation of blood through different organs are observed in the cases of the *lungs*, the *liver*, the *brain*, and the *erectile organs*. The pulmonary and portal circulations have been already alluded to (pp. 74, 75), and will be again noticed, when considering the functions of the lungs and liver.

The chief circumstances requiring notice in relation to the *cerebral circulation*, are observed in the arrangement and distribution of the vessels of the brain, and in the conditions attending the amount of blood usually contained within the cranium.

The functions of the brain seem to require that it should receive a large supply of blood. This is accomplished through the number and size of its arteries, the two internal carotids, and the two vertebrals. But it appears to be further necessary that the force with which this blood is sent to the brain should be less, or at least, subject to less variation from external circumstances, than it is in other parts. This object is effected by several provisions; such as the tortuosity of the large arteries, and their wide anastomoses in the formation of the circle of Willis, which will insure that the supply of blood to the brain may be uniform, though it may by an accident be diminished, or in some way changed, through one or more of the principal arteries. The transit of the large arteries through bone, especially the carotid canal of the temporal bone, may prevent any undue distension; and uniformity of supply is

further insured by the arrangement of the vessels in the pia mater, in which, previous to their distribution to the substance of the brain, the large arteries branch and divide into innumerable minute ramuscles and capillaries, which, after frequent communications with one another, enter the brain, and carry into nearly every part of it uniform and equable streams of blood.

The arrangement of the *veins* within the cranium is also peculiar. The large venous trunks or sinuses are formed so as to be scarcely capable of change of size; and composed as they are of the tough tissue of the dura mater, and in some instances, bounded on one side by the bony cranium, they are not compressible by any force which the fulness of the arteries might exercise through the substance of the brain; nor do they admit of distension when the flow of venous blood from the brain is obstructed.

The general uniformity in the supply of blood to the brain, which is thus secured, is well adapted, not only to its functions, but also to its condition as a mass of nearly incompressible substance placed in a cavity with unyielding walls. These conditions of the brain and skull have appeared, indeed, to some, enough to justify the opinion that the quantity of blood in the brain must be at all times the same; and that the quantity of blood received within any given time through the arteries must be always, and at the same time, exactly equal to that removed by the veins. In accordance with this supposition, the symptoms commonly referred to either excess or deficiency of blood in the brain, were ascribed to a disturbance in the balance between the quantity of arterial and that of venous blood. Some experiments performed by Dr. Kellie appeared to establish the correctness of this view. He believed that in animals bled to death, while all the other organs of the body were nearly emptied of blood, the vessels of the brain contained almost their ordinary quantity; but that if, previous to bleeding an animal, he made a hole in its cranium, and thus exposed the brain, equally with the other organs, to the

influence of atmospheric pressure, its vessels, like those of other parts of the body, were emptied as the animal bled to death. But Dr. Burrows (lxxi. May, 1843, and xcv.), having repeated these experiments, and performed additional ones, obtained different results. He found that in animals bled to death, without any aperture being made in the cranium, the brain became pale and anæmic like other parts. And in proof that, during life, the cerebral circulation is influenced by the same general circumstances that influence the circulation elsewhere, he found congestion of the cerebral vessels in rabbits killed by strangling or drowning; while in others, killed by prussic acid, he observed that the quantity of blood in the cavity of the cranium was determined by the position in which the animal was placed after death, the cerebral vessels being congested when the animal was suspended with its head downwards, and comparatively empty when the animal was kept suspended by the ears. He concluded, therefore, that although the total volume of the contents of the cranium is probably nearly always the same, yet the quantity of blood in it is liable to variation, its increase or diminution being accompanied by a simultaneous diminution or increase in the quantity of the cerebro-spinal fluid, which, by readily admitting of being removed from one part of the brain and spinal cord to another, and of being rapidly absorbed, and as readily effused, would serve as a kind of supplemental fluid to the other contents of the cranium, to keep it uniformly filled in case of variations in their quantity (see also Ecker, cxxix). But such variations occur only in abnormal conditions. In ordinary states, and in health, it is probable that the arrangements of the vessels, to which we have referred, ensure to the brain a supply of blood, which is both uniform and guarded from the accidental disturbances to which the supply for all other organs is liable, even in circumstances consistent with health.

*Erectile structures.*—The instances of greatest variation in the quantity of blood contained, at different times, in the same

organs, are found in certain structures which, under ordinary circumstances, are soft and flaccid, but, at certain times, receive an unusually large quantity of blood, become distended and swollen by it, and pass into the state which has been termed *erection*. Such structures are the corpora cavernosa and corpus spongiosum of the penis in the male, and the clitoris in the female; and, in a less degree, the nipple of the mammary gland in both sexes. The corpus cavernosum penis, which is the best example of an erectile structure, has an external fibrous membrane or sheath, from the inner surface of which numerous fine lamellæ pass into the interior of the body, dividing its cavity into small compartments which look like cells when they are inflated. Within these is situated the plexus of veins upon which the peculiar erectile property of the organ mainly depends. It consists of short veins which very closely interlace and anastomose with each other in all directions, and admit of great variation of size, collapsing in the passive state of the organ, but, for erection, capable of an amount of dilatation which exceeds beyond comparison that of the arteries and veins which convey the blood to and from them. The strong fibrous tissue lying in the intervals of the venous plexuses, and the external fibrous membrane or sheath with which it is connected, limit the distension of the vessels, and, during the state of erection, give to the penis its condition of tension and firmness. The same general condition of vessels exists in the corpus spongiosum urethræ, but around the urethra the fibrous tissue is much weaker than around the body of the penis, and around the glans there is none. The venous blood is returned from the plexuses by comparatively small veins; those from the glans and the fore part of the urethra empty themselves into the dorsal vein of the penis; those from the corpus cavernosum pass into deeper veins which issue from the corpora cavernosa at the crura penis; and those from the rest of the urethra and bulb pass more directly into the plexus of the veins about the prostate. For all these veins one condition is the same; namely, that they

are liable to the pressure of muscles when they leave the penis. The vena dorsalis penis may be compressed by the uniting tendons of the ischio-cavernosi; the crura penis, and the veins issuing from them, are under the same muscles; and the veins of the bulb are subject to the compression of the bulbo-cavernosi (see Krause, lxxx. 1837; Kobelt, cxxvii. and xxv. 1843-4, p. 58).

Erection results from the distension of the venous plexuses with blood. The principal exciting cause in the erection of the penis is nervous irritation, originating in the part itself, or derived from the brain and spinal cord. The nervous influence is communicated to the penis by the pudic nerves, which ramify in its vascular tissue: and Guenther (xcvi. 1828, p. 364) has observed, that, after their division in the horse, the penis is no longer capable of erection. It affords a good example of the subjection of the circulation in an individual organ to the influence of the nerves; but the mode in which they excite a greater influx of blood is not with certainty known.

The most probable explanation is that offered by Professor Kölliker, who ascribes the distension of the venous plexuses to the influence of organic muscular fibres, which he finds in abundance in the corpora cavernosa of the penis, from the bulb to the glans, also in the clitoris and other parts capable of erection. While erectile organs are flaccid and at rest, these contractile fibres exercise an amount of pressure on the plexuses of vessels distributed amongst them, sufficient to prevent their distension with blood. But when, through the influence of their nerves, these parts are stimulated to erection, the action of these fibres is suspended, and the plexuses thus liberated from pressure, yield to the distending force of the blood, which, probably, at the same time arrives in greater quantity, owing to a simultaneous dilatation of the arteries of the parts, and thus the plexuses become filled, and remain so until the stimulus to erection subsides, when the organic muscular fibres again contract, and so gradually expel the excess of blood from the previously distended vessels. The influence

of cold in producing extreme contraction and shrinking of erectile organs, and the opposite effect of warmth in inducing fulness and distension of these parts, are among the arguments used by Kölliker in support of this opinion (cxci.).

The accurate dissections and experiments of Kobelt (cxxvii.), extending and confirming those of Le Gros Clark (lxxi. vol. xviii. p. 437) and Krause (lxxx. 1837), have shewn, that this influx of the blood, however explained, is the first condition necessary for erection, and that through it alone, much enlargement and turgescence of the penis may ensue. But the erection is probably not complete, nor maintained for any time except when, together with this influx, the muscles already mentioned contract, and by compressing the veins, stop the efflux of blood, or prevent it from being as great as the influx.*

It appears to be only the most perfect kind of erection that needs the help of muscles to compress the veins; and none such can assist the erection of the nipples, or that amount of turgescence, just falling short of erection, of which the spleen and many other parts are capable. For such turgescence nothing more seems necessary than a large plexiform arrangement of the veins, and such arteries as may admit, upon local occasions, augmented quantities of blood.

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## CHAPTER VI.

### RESPIRATION.

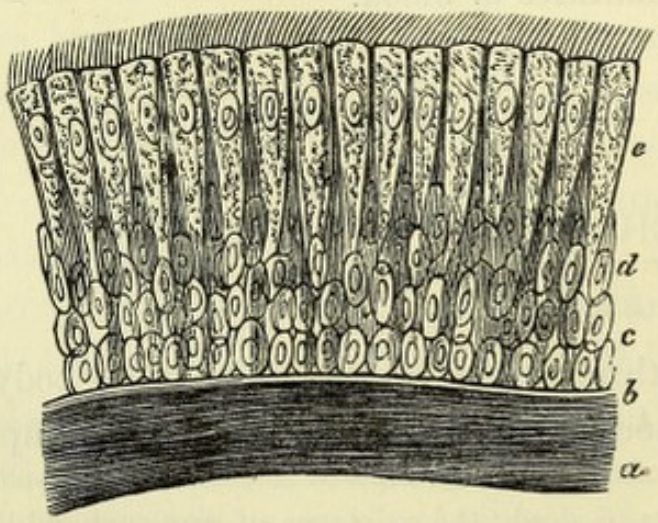
As the blood circulates through the various parts of the body, and fulfils its office by nourishing the several tissues and sup-

* Kölliker, however, seems to doubt the existence of any such additional influence in the production of erection, and believes that the mere accumulation of blood in the various plexuses, in consequence of the relaxation of the muscular fibres by which they are surrounded, is sufficient to produce the distension and firmness characteristic of the erectile state.

plying to secreting organs the materials necessary for their different secretions, it is deprived of part of its nutritive constituents, and becomes charged with impurities resulting from the deterioration of the tissues. It is, therefore, necessary that fresh supplies of nutriment should be continually added to the blood, and that provision should be made for the removal of the impurities. The first of these objects is accomplished by the processes of digestion and absorption. The second is principally effected by the agency of the various excretory organs through which are removed the several impurities with which the blood is charged, whether these impurities are derived altogether from the degeneration of tissues, or in part also from the elements of unassimilated food. One of the most important and abundant of the impurities is carbonic acid, the removal of which and the introduction of fresh quantities of oxygen, constitute the chief purpose of respiration—a process which, because of its intimate relation to the circulation, may be considered here, rather than with the other excretory functions.

### *Structure of the Lungs.**

*Fig.* 14.




The respiratory process in man, and in all Mammalia, is chiefly carried on in the minute cavities within the lungs, called *air-cells* or pulmonary vesicles. Each lobule, or small subdivision of the lung, consists of a collection of such air-

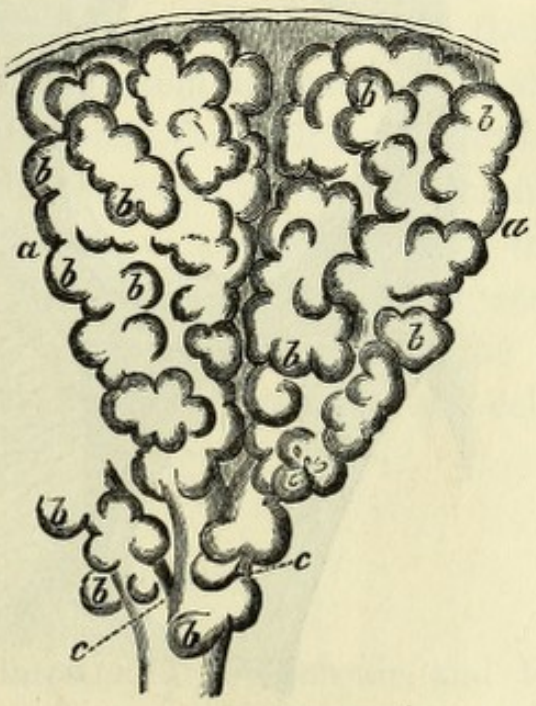
* Among the most recent works on the structure of the lungs, are those by Rainey (xli. vol. 28); Addison (xliii. 1842); Kölliker (ccvi., ccxii., and ccxviii.); T. Williams (lxxiii., Art. *Organs of Respiration*); and H. Waters (ccxxvii).

† Fig. 14. Ciliary epithelium of the human trachea magnified 350

cells, clustered upon and opening into minute branches of the bronchial tubes, and having their walls overlaid with capillaries derived from the terminal branches of the pulmonary artery.

The bronchial tube belonging to each lung passes into its substance, dividing and subdividing, but without anastomosis, and sending branches to every part of the organ. All the larger branches have walls formed of tough membrane with organic-muscular circular fibres, giving them some power of spontaneous contraction, portions of cartilaginous rings by which they are held open, and longitudinal bundles of elastic tissue for greater power of recoil after extension: they are lined with mucous membrane, the surface of which, like that of the trachea, is covered with vibratile ciliary epithelium (fig. 14). But when the bronchi, by successive branchings, are reduced to about $\frac{1}{100}$ of an inch in diameter, they lose these structures, and their walls are formed only of a tough, elastic membrane, with traces of fibrous, probably muscular, structure, over which the capillaries are spread in a very dense network, and on various parts of which air-cells irregularly open. Tubes of this kind are named by Mr. Rainey *intercellular passages*. The air-cells opening into them may be

*Fig.* 15.*

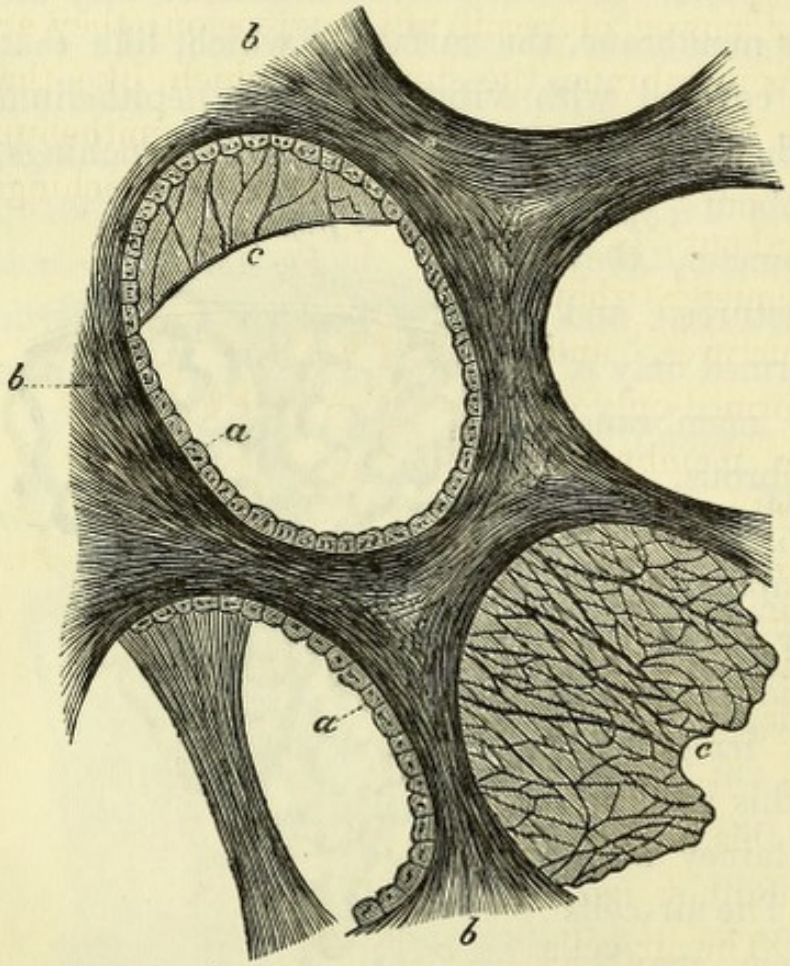



diameters. *a*. Layer of longitudinally arranged elastic fibres; *b*. Basement membrane; *c*. Deepest cells, circular in form; *d*. Intermediate elongated cells; *e*. Outermost layer of cells fully developed and bearing cilia. (After Kölliker, ccvi.)

* Fig. 15. Two small pulmonary lobules, *a a*, with air-cells, *b b*, and the ultimate bronchial tubes (or intercellular passages), *c c*, with which the air-cells communicate. From a new-born child. (After Kölliker, ccvi.)

placed singly on their walls, like recesses from them; but more often are arranged in rows like minuter sacculated tubes; so that a succession or series of cells, all opening into one another, open by a common orifice into the tube (fig. 15). The cells are of various forms, according to the mutual pressure to which they are subject; their walls are nearly in contact, and they vary from $\frac{1}{120}$ to $\frac{1}{1200}$ of an inch in diameter (Moleschott, cxxi). Their walls are formed of fine membrane, similar to that of the intercellular passages, and continuous with it, which is folded on itself so as to form a sharp-edged border at each circular orifice of communication between contiguous air-cells, or between the cells and the bronchial passages. Numerous fibres of elastic tissue are spread out between contiguous air-cells, and many of these are attached to the outer surface of the fine mem-

*Fig.* 16.*




* Fig. 16. Air-cells of lung, magnified 350 diameters. *a.* Epithelial lining of the cells; *b.* Fibres of elastic tissue; *c.* Delicate membrane of which the cell-wall is constructed, with elastic fibres attached to it. (After Kölliker, ccvi.)

brane of which each cell is composed, imparting to it additional strength, and the power of recoil after distension (fig. 16, *b* and *c*). The cells are lined by a layer of epithelium of the pavement or tesselated variety (see fig. 16, *a*). Outside the cells, a network of pulmonary capillaries is spread out so densely, that the interspaces or meshes are even narrower than the vessels, which are, on an average, $\frac{1}{3000}$ of an inch in diameter. Between the atmospheric air in the cells and the blood in these vessels nothing intervenes but the thin membranes of the cells and capillaries, and the delicate epithelial lining of the former; and the exposure of the blood to the air is the more complete, because the folds of membrane between contiguous cells, and often the spaces between the walls of the same, contain only a single layer of capillaries, both sides of which are thus at once exposed to the air.

The cells situated nearest to the centre of the lung are smaller, and their networks of capillaries are closer than those nearer to the circumference, in adaptation to the more ready supply of fresh air to the central than the peripheral portion of the lungs. The cells of adjacent lobules do not communicate; and those of the same lobule, or proceeding from the same intercellular passage, do so as a general rule only near angles of bifurcation; so that, when any bronchial tube is closed or obstructed, the supply of air is lost for all the cells opening into it or its branches.

### *Movements of Respiration.*

The movements for taking into the lungs fresh air, and for expelling from them the air that has been changed by the respiratory process, are those of inspiration and expiration. The former is performed by the contraction of muscles bounding or attached to the exterior of the chest; the latter, chiefly and usually, by the elastic contraction or recoil of the lungs and the walls of the chest, after they have been dilated in the act of inspiration.

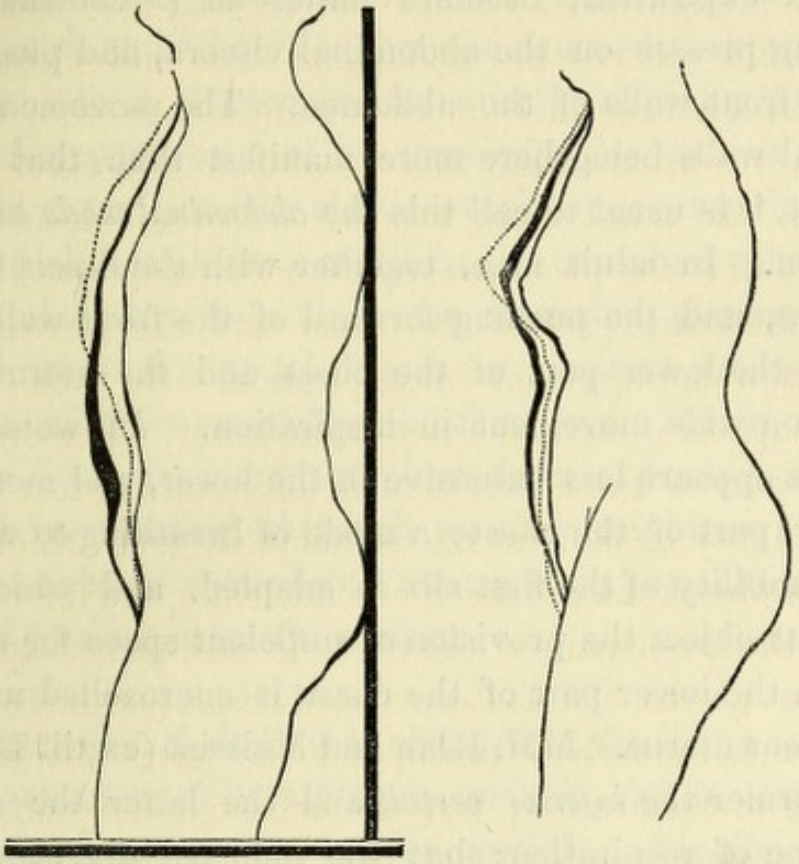
The chest is a cavity closed on every side from the entrance of air; its immediate boundary is formed by its lining membrane, the pleura; its walls, external to the pleura, are partly osseous and unyielding, though moveable, partly muscular, partly elastic. It is filled by the lungs and heart and their larger vessels, and these fill it equally in all its alterations of size; when it enlarges, they receive more air and blood; when it contracts, air and blood pass out of them; and the lungs and part of the heart are always in contact with every part of its internal surface. The changes produced by the respiratory movements on the circulation of blood have been noticed already (p. 133); the much greater changes of the air will now be alone considered.

Air, as already said, fills all the air-tubes and cells of the lungs; and through their medium, the pressure of the atmosphere is communicated, through the open glottis, to the whole of the interior of the cavity of the chest, and balances the pressure of the atmosphere on the exterior of the chest. The force, therefore, which is required for the expansion of the chest in inspiration is not more than is necessary for moving the weight of its walls and those of the abdomen, and overcoming their elasticity and that of the lungs. The expressions which imply the necessity of forming a vacuum in the chest to draw in air, are inaccurate or exaggerated; the pressure of the atmosphere on both the inside and outside of the chest being equal, its walls are free to move so long as the glottis is open. When they are raised, so as to expand the chest, the pressure on the exterior of the lungs is made somewhat less than that of the atmospheric air on their interior: the excess of pressure, therefore, impels more air into them through the trachea. When, on the other hand, the walls of the chest contract, or allow the elastic tissue of the lungs and pulmonary pleura to contract, the pressure is greater on the exterior than on the interior of the lungs, and air is forced out of them through the trachea.

In its enlargement in inspiration the capacity of the chest

is commonly increased in all directions; and chiefly in its vertical diameter and at its posterior part, so as to ensure the

*Fig.* 17.* *Fig.* 18.†



expansion of the great masses of lung which lie in the hollows at the back of the chest, by the sides of the spine. But its

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* Fig. 17. The changes of the thoracic and abdominal walls of the male during respiration. The back is supposed to be fixed in order to throw forward the respiratory movement as much as possible. The outer black continuous line in front represents the ordinary breathing movement: the anterior margin of it being the boundary of *inspiration*, the posterior margin the limit of *expiration*. The line is thicker over the abdomen, since the ordinary respiratory movement is chiefly abdominal: thin over the chest, for there is less movement over that region. The dotted line indicates the movement on deep inspiration, during which the sternum advances while the abdomen recedes.

† Fig. 18. The respiratory movement in the female. The lines indicate the same changes as in the last figure. The thickness of the continuous line over the sternum shews the larger extent of the ordinary breathing movement over that region in the female than in the male.

mode of increase presents some peculiarities in different persons and circumstances. In young children, the inspiration is effected almost entirely by the diaphragm, which being highly arched in expiration, becomes flatter as it contracts, and descending presses on the abdominal viscera, and pushes forward the front walls of the abdomen. The movement of the abdominal walls being here more manifest than that of any other part, it is usual to call this the *abdominal mode* or *type* of respiration. In adult men, together with the descent of the diaphragm, and the pushing forward of the front wall of the abdomen, the lower part of the chest and the sternum are subject to a wide movement in inspiration. In women, the movement appears less extensive in the lower, and more so in the upper, part of the chest; a mode of breathing to which a greater mobility of the first rib is adapted, and which may have for its object the provision of sufficient space for respiration when the lower part of the chest is encroached upon by the pregnant uterus. MM. Beau and Maissiat (cxxii. 1842-3), call the former the *inferior costal*, and the latter the *superior costal*, type of respiration; but the annexed diagrams from Mr. Hutchinson's paper (xli. vol. xxix.) will explain the difference better than the names will, for they imply a greater diversity than naturally exists in the modes of inspiration.

From the enlargement produced in inspiration, the chest and lungs return, with expiration, by their elasticity.* The costal cartilages are the chief seats of elastic power in the walls of the

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* For an account of the particular muscles engaged in inspiration, see the article *Thorax*, by Mr. Hutchinson, in the Cyclopædia of Anatomy; a paper on the Movements of Respiration, by Dr. Sibson, in the Medico-Chirurgical Transactions for 1848; and, as well as to these, the student may refer to Mr. Hutchinson's paper in the twenty-ninth volume of the Medico-Chirurgical Transactions; Dr. Sibson's papers in the Philosophical Transactions for 1846, and the forty-first volume of the Medical Gazette; Dr. J. Reid's article *Respiration* in the Cyclopædia of Anatomy; and the papers of MM. Beau and Maissiat (cxxii. 1842 and 1843).

chest, and add to the force of an ordinary expiration, *i.e.*, of such an one as is made in tranquil breathing. But the walls of the chest hinder deeper expirations, such as are made in straining, coughing, and the like; for these, muscular efforts are required, and when the chest is contracted or compressed by those efforts it recovers its average capacity by its elasticity. Independently of its elasticity, the walls of the chest follow, in expiration, the elastic recoil or contraction of the lungs, which have elastic tissue in the bronchial tubes, on and between the air-cells, and in the investing pleura, and are always kept on the stretch, ready to contract as soon as the muscular effort for expanding the chest ceases, contracting with the more force the more they have been expanded, and never in health contracting so much as they might, or as they do when the chest is opened and atmospheric pressure is directly admitted to their external surface.

The quantity of air that is changed in the lungs in each act of ordinary tranquil breathing is variable, and is very difficult to estimate, because it is hardly possible to breathe naturally while, as in an experiment, one is attending to the process. The best estimate, perhaps, is that by Mr. Coathupe (xciii. 1839), who states the quantity at from twenty to twenty-five cubic inches; and this is probably as near as possible to the truth in the case of healthy young and middle-aged men; but Bourgery (cxxii. 1843) is perhaps right in saying that old people, even in health, habitually breathe more deeply, and change in each respiration a larger quantity of air than younger persons do.

This quantity, being that habitually and almost uniformly changed in breathing, is called by Mr. Hutchinson (xli. vol. 29) *breathing air*. The quantity over and above this which a man can draw into the lungs in the deepest inspiration he names *complemental air:* its amount is various, as will be presently shewn. After ordinary expiration, such as that which expels the *breathing air*, a certain quantity of air re-

mains in the lungs, which may be expelled by a forcible and deeper expiration: this he terms *reserve air*. But, even after the most violent expiratory effort, the lungs are not completely emptied; a certain quantity always remains in them, over which there is no voluntary control, and which may be called *residual air*. Its amount depends in great measure on the absolute size of the chest, and has been variously estimated at from forty to two hundred and sixty cubic inches.

The greatest respiratory capacity of the chest is indicated by the quantity of air which a person can expel from his lungs by a forcible expiration after the deepest inspiration that he can make. Mr. Hutchinson names this the *vital capacity:* it expresses the power which a person has of breathing in the emergencies of active exercise, violence, and disease; and in healthy men it varies according to *stature, weight,* and *age.*

It is found by Mr. Hutchinson, from whom most of our information on this subject is derived, that at a temperature of 60° F. 225 cubic inches is the average *vital capacity* of a healthy person, five feet seven inches in height. For every inch of height above this standard the capacity is increased, on an average, by eight cubic inches; and for every inch below, it is diminished by the same amount. This relation of capacity to height is quite independent of the absolute capacity of the cavity of the chest; for the cubic contents of the chest do not always, or even generally, increase with the stature of the body; and a person of small absolute capacity of chest may have a large capacity of respiration, and *vice versâ*. The capacity of respiration is determined only by the mobility of the walls of the chest; but why this mobility should increase in a definite ratio with the height of the body is yet unexplained, and must be difficult of solution, seeing that the height of the body is chiefly determined by that of the legs, and not by the height of the trunk or the depth of the chest.

But the vast number of observations made by Mr. Hutchinson seem to leave no doubt of the fact as stated above.

The influence of *weight* on the capacity of respiration is less manifest and considerable than that of height: and it is difficult to arrive at any definite conclusions on this point, because the natural average weight of a healthy man in relation to stature has not yet been determined. As a general statement, however, it may be said, that the capacity of respiration is not affected by weights under 161 pounds, or 11½ stones; but, that above this point, it is diminished at the rate of one cubic inch for every additional pound up to 196 pounds, or 14 stones; so that, for example, while a man of five feet six inches, and weighing less than 11½ stones, should be able to expire 217 cubic inches, one of the same height, weighing 12½ stones, might expire only 203 cubic inches.

By *age* the capacity appears to be increased from about the fifteenth to the thirty-fifth year, at the rate of five cubic inches per year; from thirty-five to sixty-five it diminishes at the rate of about one and a-half cubic inch per year; so that the capacity of respiration of a man sixty years old would be about 30 cubic inches less than that of a man forty years old, of the same height and weight.

Mr. Hutchinson's observations were made almost exclusively on men; and his conclusions are, perhaps, true of them alone; for women, according to Bourgery, have only half the capacity of breathing that men of the same age have.

The *number* of respirations in a healthy adult person usually ranges from fourteen to eighteen per minute. According to Mr. Hutchinson, the *force* with which the inspiratory muscles are capable of acting is greatest in individuals of the height of from five feet seven inches to five feet eight inches, and will elevate a column of three inches of mercury. Above this height, the force decreases as the stature increases; so that the average of men of six feet can elevate only about two and a half inches of mercury. The force manifested in the strongest expiratory acts is, on the average, one-third greater

than that exercised in inspiration. But this difference is in great measure due to the power exerted by the elastic reaction of the walls of the chest; and it is also much influenced by the disproportionate strength which the expiratory muscles attain, through being called into use for other purposes than that of simple expiration. The force of the inspiratory act is, therefore, better adapted than that of the expiratory for testing the muscular strength of the body.

Much of the force exerted in inspiration is employed in overcoming the resistance offered by the elasticity of the walls of the chest and of the lungs. Mr. Hutchinson estimated the amount of this elastic resistance, by observing the elevation of a column of mercury raised by the return of air forced, after death, into the lungs, in quantity equal to the known capacity of respiration during life; and he calculated that, in a man capable of breathing 200 cubic inches of air, the muscular power expended upon the elasticity of the walls of the chest, in making the deepest inspiration, would be equal to the raising of at least 301 pounds avoirdupois. In tranquil respiration, supposing the amount of breathing air to be twenty cubic inches, the resistance of the walls of the chest would be equal to lifting more than 200 pounds. The elastic force exerted in ordinary expiration must, therefore, be much greater than enough to lift this weight; because in it the elastic force of the lungs is also in action,—a force which is not included in these estimates, because the lungs were in both cases burst by the air forced into them.

It is probable, that in the ordinary quiet respiration, which is performed without consciousness or effort of the will, the only forces engaged are those of the inspiratory muscles, and the elasticity of the walls of the chest and the lungs. And it is not known under what circumstances the contractile power which the bronchial tubes possess, by means of their organic muscular fibres, is brought into action. It is possible, as Dr. R. Hall (cc.) maintained, that it may exist in expiration; but it is more likely that its chief purpose is to regulate and

adapt, in some measure, the quantity of air admitted to the lungs, and to each part of them, according to the supply of blood. Another purpose probably served by the muscular fibres of the bronchial tubes is that of contracting upon and gradually expelling collections of mucus, which may have accumulated within the tubes, and cannot be ejected by forced expiratory efforts, owing to collapse or other morbid conditions of the portion of lung proceeding from the obstructed tubes (Dr. W. T. Gairdner, clxxxix. May, 1851).

The muscular action in the lungs, morbidly excited, is probably the chief cause of the phenomena of spasmodic asthma. It may be demonstrated by galvanizing the lungs shortly after taking them from the body. Under such a stimulus, they contract so as to lift up water placed in a tube introduced into the trachea (C. J. B. Williams, cxxxi. p. 588); and Volkmann (xv. art. *Nervenphysiologie,* p. 586), has shewn that they may be made to contract by stimulating their nerves. He tied a glass tube, drawn fine at one end, into the trachea of a beheaded animal; and when the small end was turned to the flame of a candle, he galvanized the pneumogastric trunk. Each time he did so, the flame was blown, and once it was blown out.

The changes of the air in the lungs effected by these respiratory movements are assisted by the various conditions of the air itself. According to the law observed in the diffusion of gases, the carbonic acid evolved in the air-cells will, independently of any respiratory movement, tend to leave the lungs, by diffusing itself into the external air, where it exists in less proportion; and according to the same law, the oxygen of the atmospheric air will tend of itself towards the air-cells in which its proportion is less than it is in the air in the bronchial tubes or in that external to the body. But for this tendency in the oxygen and carbonic acid to mix uniformly, within and without the lungs, the *reserve* and *residual* air would, probably, be very injuriously charged with carbonic acid; for the respiratory movements alone are not enough to empty the

air-cells, and perhaps expel only the air which lies in the larger bronchial tubes. Probably also the change is assisted by the different temperature of the air within and without the lungs; and by the action of the cilia on the mucous membrane of the bronchial tubes, the continual vibrations of which may serve to prevent the adhesion of the air to the moist surface of the membrane.

### *Movement of the Blood in the Respiratory Organs.*

To meet the air thus alternately moved into and out of the air-cells and minute bronchial tubes, the blood is propelled from the right ventricle through the pulmonary capillaries in steady streams, and slowly enough to permit every minute portion of it to be for a few seconds exposed to the air, with only the thin walls of the capillary vessels and air-cells intervening. The pulmonary circulation is of the simplest kind; for the pulmonary artery branches regularly; its successive branches run in straight lines, and do not anastomose; the capillary plexus is uniformly spread over the air-cells and intercellular passages; and the veins derived from it proceed in a course as simple and uniform as that of the arteries, their branches converging but not anastomosing. The veins have no valves, or only small imperfect ones prolonged from their angles of junction, and incapable of closing the orifice of either of the veins between which they are placed. The pulmonary circulation also is unaffected by changes of atmospheric pressure, and is not exposed to the influence of the pressure of muscles: the force by which it is accomplished, and the course of the blood, are alike simple.

The blood carried through the pulmonary artery, being venous till it comes to the capillaries, is unfit for the nutrition of any parts of the lungs, except those in which it flows through the capillaries; to these it probably supplies nutritive materials as soon as it is itself arterialized. For the nutrition of the rest of the lungs, including the pleura, interlobular

tissue, bronchial tubes and glands, and the walls of the larger blood-vessels, a special supply of arterial blood is furnished through one or two bronchial arteries, the branches of which ramify in all these parts. The blood of the bronchial artery when, having served for the nutrition of these parts, it has become venous, is carried, partly, into the branches of a bronchial vein, distributed in the parts about the root of the lung, and partly into the small branches of the pulmonary artery, or, more directly, into the pulmonary capillaries, whence, being with the rest of the blood arterialized, it is carried to the pulmonary veins and left side of the heart.

### *Changes of the Air in Respiration.*

By their contact in the lungs the composition of both air and blood is changed. The alterations of the former being manifest, simpler than those of the latter, and in some degree illustrative of them, may be considered first.

The *atmosphere* we breathe has, in every situation in which it has been examined in its natural state, a nearly uniform composition. It appears to be a mixture of oxygen, nitrogen, carbonic acid, and watery vapour. Of every 100 volumes of pure atmospheric air, 79 volumes (on an average) consist of nitrogen, the remaining 21 of oxygen; but the proportions of these gases are subject to variations of 2 or 3 parts in 1000, in situations where the oxygen is much exposed to absorption, as over the sea when there is no wind (Lewy, xviii. 1842). The proportion of carbonic acid is extremely small; 10,000 volumes of atmospheric air contain, according to M. de Saussure, only 4·15 of carbonic acid. In the open country, he found the maximum proportion of this gas to be 5·74, the minimum 3·15 in 10,000 parts. In the town of Geneva, the air contained 0·31 more carbonic acid than in the country. M. Boussingault, however, has lately found (xii. 1844), from numerous analyses, which are confirmed by those of M. Lewy, that the quantity of carbonic acid in the air of Paris (which

may be taken as an example of a large town), is not above the average of the quantity contained in the air of the country. This average he finds to be 3·97 volumes in 10,000: and his estimate may be considered generally true, except for localities, such as mines, crowded rooms, volcanic districts, and others, in which large quantities of carbonic acid are constantly exhaling.

Dr. Frankland has lately shewn, from the analysis of air obtained from the top of Mont Blanc, that the per centage of carbonic acid is generally, but not invariably, greater in the higher regions of the atmosphere (lxii. 1860.)

The quantity of watery vapour varies greatly, according to the temperature and other circumstances, but some is never absent from the atmosphere. Besides these, its constant constituents, the atmosphere usually contains minute fractional quantities of ammonia, and other accidental substances; but, as far as is at present known, none of these have any particular relation to the respiratory process; and the consideration of them may therefore be omitted.

The changes produced by respiration on the atmospheric air are that 1, it is warmed; 2, its carbonic acid is increased; 3, its oxygen is diminished; 4, its watery vapour is increased.

1. The expired air, heated by its contact with the interior of the lungs, is (at least in most climates) hotter than the inspired air. Its temperature varies between 97° and 99½°, the lower temperature being observed when the air has remained but a short time in the lungs rather than when it was inhaled at a very low temperature; for whatever the temperature when inhaled may be, the air nearly acquires that of the blood before it is expelled from the chest.

2. *The carbonic acid in respired air is always increased;* but the quantity exhaled in a given time is subject to change from various circumstances. It may be stated, as a general

average, deduced from the results of experiments by Valentin and Brunner (iv. vol. i. 547), that under ordinary circumstances, the quantity of this gas exhaled into the air breathed by a healthy adult man amounts to 1345·3 cubic inches, or about 636 grains per hour. According to this estimate, which corresponds very closely with the one furnished by Sir H. Davy, and does not widely differ from those obtained by Allen and Pepys, and by Lavoisier, the weight of carbon excreted from the lungs is about 173 grains per hour, or 8 ounces in the course of twenty-four hours. Andral and Gavarret (cix.), calculate the average quantity of carbon excreted from the lungs of a healthy adult man at 9 ounces per day. Mr. Coathupe (xciii. 1839) makes it scarcely 5 ounces; while Liebig (xi. 3rd edit. p. 13) estimates the total quantity excreted from the lungs and skin together at 13·9 ounces. Some of these discrepancies may be due to the variations to which the exhalation of carbonic acid is liable in different circumstances; for even in health the quantity varies according to age, sex, diversities in the respiratory movements, external temperature, the degree of purity of the respired air, and other circumstances. Each of these circumstances deserves a brief notice, because they afford evidence concerning either the sources of the carbonic acid exhaled, or the mode in which it is separated from the blood.

*a. Influence of Age and Sex.*—According to Andral and Gavarret (cix.) the quantity of carbonic acid exhaled into the air breathed by males regularly increases from eight to thirty years of age; from thirty to forty it is stationary or diminishes a little; from forty to fifty the diminution is greater; and from fifty to extreme age it goes on diminishing, till it scarcely exceeds the quantity exhaled at ten years old. In females (in whom the quantity exhaled is always less than in males of the same age) the same regular increase in quantity goes on from the eighth year to the age of puberty, when the quantity abruptly ceases to increase, and remains stationary

so long as they continue to menstruate. When, however, menstruation has ceased, either in advancing years, or in pregnancy, or morbid amenorrhœa, the exhalation of carbonic acid again augments; but when menstruation ceases naturally, it soon decreases again at the same rate as it does in old men.

*b. Influence of Respiratory Movements.*—According to Dr. Vierordt (ex.) the more quickly the movements of respiration are performed, the smaller is the proportionate quantity of carbonic acid contained in each volume of the expired air. Thus he found that, with six respirations per minute, the quantity of expired carbonic acid was 5·528 per cent.; with twelve respirations, 4·262 per cent.; with twenty-four, 3·355; with forty-eight, 2·984; and with ninety-six, 2·662. Although, however, the proportionate quantity of carbonic acid is thus diminished during frequent respiration, yet the absolute amount exhaled into the air within a given time is increased thereby, owing to the larger quantity of air which is breathed in the time. This is the case, whether the respiration be voluntarily accelerated, or naturally increased in frequency, as it is after feeding, active exercise, etc. By diminishing the frequency, and increasing the depth of respiration, the percentage proportion of carbonic acid in the expired air is diminished; being in the deepest respiration as much as 1·97 per cent. less than in ordinary breathing. But for this proportionate diminution also, there is a full compensation in the greater total volume of air which is thus breathed. Finally, the last half of a volume of expired air contains more carbonic acid than the half first expired; a circumstance which is explained by the one portion of air coming from the remote parts of the lungs, where it has been in more immediate and prolonged contact with the blood than the other has, which comes chiefly from the larger bronchial tubes.

*c. Influence of external Temperature.* — The observations made by Vierordt at various temperatures between 38° F. and

75° F. shew, for warm-blooded animals, that within this range, every rise equal to 10° F. causes a diminution of about two cubic inches in the quantity of carbonic acid exhaled per minute. Letellier (xii. 1845), from experiments performed on animals at much higher and lower temperatures than the above, also found that the higher the temperature of the respired air (as far as 104° F.), the less is the amount of carbonic acid exhaled into it, whilst the nearer it approaches zero the more does the carbonic acid increase. The greatest quantity exhaled at the lower temperatures he found to be about twice as much as the smallest exhaled at the higher temperatures.

*d. Purity of the respired Air.*—The average quantity of carbonic acid given out by the lungs constitutes about 4·48 per cent. of the expired air; but if the air which is breathed be previously impregnated with carbonic acid (as is the case when the same air is frequently respired), then the quantity of carbonic acid exhaled becomes much less. This is shown by the results of two experiments performed by Allen and Pepys (xliii. 1808-9). In one, in which fresh air was taken in at each respiration, thirty-two cubic inches of carbonic acid were exhaled in a minute; whilst, in the other, in which the same air was respired repeatedly, the quantity of carbonic acid emitted in the same time was only 9·5 cubic inches. They found also, that, however often the same air may be respired, even if until it will no longer sustain life, it does not become charged with more than 10 per cent. of carbonic acid. The necessity of a constant supply of fresh air, by means of ventilation, through rooms in which many persons are breathing together, or in which, from any other source, much carbonic acid is evolved, is thus rendered obvious; for even when the air is not completely irrespirable, yet in the same proportion as it is already charged with carbonic acid, does the further extrication of that gas from the lungs suffer hindrance.

The *period of day* seems to exercise a slight influence on the amount of carbonic acid exhaled in a given time, though

beyond the fact that the quantity exhaled is much less by night than by day, we are scarcely yet in a position to state that variations in the amount exhaled occur at uniform periods of the day, independent of the influence of other circumstances. By the *use of food* the quantity is increased, whilst by fasting it is diminished: and, according to Regnault and Reiset, it is greater when animals are fed on farinaceous food than when fed on meat. Spirituous drinks, especially when taken on an empty stomach produce an immediate and marked diminution in the quantity of this gas exhaled. *Bodily exercise*, in moderation, increases the quantity to about one-third more than it is during rest: and for about an hour after exercise, the volume of the air expired in the minute is increased about 118 cubic inches: and the quantity of carbonic acid about 7·8 cubic inches per minute. During *sleep*, on the other hand, there is a considerable diminution in the quantity of this gas evolved; a result probably in great measure dependent on the tranquillity of the breathing: directly after waking, there is a great, though quickly transitory, increase in the amount exhaled. A larger quantity is exhaled when the barometer is low than when it is high.

3. *The Oxygen in respired air is always less* than in the same air before respiration, and its diminution is generally proportionate to the increase of the carbonic acid. The experiments of Valentin and Brunner (iv. Bd. i) seem to show that for every volume of carbonic acid exhaled into the air, 1·17421 volumes of oxygen are absorbed from it: and that when the average quantity of carbonic acid, *i.e.*, 1345·3 cubic inches, or 635·85 grains, is exhaled in the hour, the quantity of oxygen absorbed in the same time is 1583·6 cubic inches or 541·5 grains. According to this estimate, there is more oxygen absorbed than is exhaled with carbon in the carbonic acid; for oxygen combines with carbon to form carbonic acid without change of volume; and to this general conclusion, namely, that the volume of air expired in a given time is less than that of the air inspired (allowance being made for

the expansion in being heated), and that the loss is due to a portion of oxygen absorbed and not returned in the exhaled carbonic acid, all observers agree, though as to the actual quantity of oxygen so absorbed they differ even widely.

The quantity of oxygen that does not combine with the carbon given off in carbonic acid from the lungs, is probably disposed of in forming some of the carbonic acid and water given off from the skin, and in combining with sulphur and phosphorus to form part of the acids of the sulphates and phosphates excreted in the urine, and probably also, from the experiments of Dr. Bence Jones (vi. April, 1851, and lxxxviii. August 30, 1851), with the nitrogen of the decomposing nitrogenous tissues.

The quantity of oxygen consumed seems to vary much not only in different individuals, but in the same individual at different periods: thus it is considerably influenced by food, being greater in dogs when fed on farinaceous than on animal food, and much diminished during fasting, while it varies at different stages of digestion. Animals of small size consume a relatively much greater amount of oxygen than larger ones. The quantity of oxygen in the atmosphere surrounding animals, appears to have very little influence on the amount of this gas absorbed by them, for the quantity consumed is not greater even though an excess of oxygen be added to the atmosphere experimented with (Regnault and Reiset, cxc. July, 1850, p. 252).

Valentin and Brunner's estimates of the interchange of the oxygen and carbonic acid in respiration, led them to believe that the exchanged quantities of the two gases are always in the proportion of their *diffusion-volumes;* a conclusion which, if it were established, would justify us in explaining the process of respiration as one due only to the properties of the gases, and their tendency to diffuse or mingle with one another in certain fixed proportions by volume. But the grounds are not yet strong enough for so weighty a conclu-

sion; and against it appear the many instances of deviation from the law, which seem proved by good experiments.* If the exchange of gases were according to the law of diffusion, their proportions ought never to vary; however much the circumstances of the general economy might change the quantity of one (as of the carbonic acid in the instances already quoted), the quantity of the other should be equally and at the same time changed. Whereas, in many experiments, and even in some of Valentin's, the proportion of oxygen absorbed has been less or more than it should have been according to the law of diffusion. Especially, the experiments of Dulong and Despretz seemed to shew, that in Carnivora, the oxygen absorbed always bears a larger proportion to the carbonic acid evolved than it does in Herbivora; and the recent careful experiments of Regnault and Reiset (xviii. 1848) confirm this, while they in no case shew such a proportion between the gases exchanged as, according to the law of diffusion, there should be. They shew, that in the dog for every 100 parts of carbonic acid formed in twenty-four hours, 134·3 parts of oxygen were, on the average, absorbed; and in the rabbit and hen for every 100 parts of carbonic acid, 109·34 parts of oxygen; while according to the diffusion-law, the proportion should be always 117·42 parts of oxygen to 100 of carbonic acid.

It may be added, that the conditions of the gases engaged in respiration are not those in which the law of diffusion would exactly hold. The law requires that both gases should be free and under equal pressure; while, in the actual case, the gas in the blood is dissolved, under pressure, and separated by a membrane from that into which it is to diffuse. It is possible that these peculiarities of the conditions may account for the deviations from the law while it is really in operation; but

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* The objections to Valentin's theory, and his answers to them, are all in his Annual Reports on Physiology in Canstatt's Jahresberichte since 1843.

many more facts than are yet ascertained will be necessary to prove this.

*The Nitrogen of the atmosphere*, in relation to the respiratory process, is supposed to serve only mechanically, by diluting the oxygen, and moderating its action upon the system. This purpose, or the mode of expressing it, has been lately denied by Liebig (xi. 3rd edit. p. 184) on the ground that if we suppose the nitrogen removed, the amount of oxygen in a given space would not be altered. But although it be true that if all the nitrogen of the atmosphere were removed, and not replaced by any other gas, the oxygen might still extend over the whole space at present occupied by the mixture of which the atmosphere is composed; yet since, under ordinary circumstances, oxygen and nitrogen, when mixed together in the ratio of one volume to four, produce a mixture which occupies precisely five volumes, with all the properties of atmospheric air, it must result that a given volume of atmosphere drawn into the lungs contains four-fifths less weight of oxygen than an equal volume composed entirely of oxygen. The greater rapidity and brilliancy with which combustion goes on in an atmosphere of oxygen than in one of common air, and the increased rapidity with which the ordinary effects of respiration are produced when oxygen instead of atmospheric air is breathed, seem to leave no doubt that the nitrogen with which the oxygen of the atmosphere is mixed has the effect of diluting this gas, in the same sense and degree as one part of alcohol is diluted when mixed with four parts of water.

It has been often discussed, whether nitrogen is ever absorbed by or exhaled from the lungs during respiration. That it may, in some conditions, be exhaled is proved by experiments of Allen and Pepys, who found that when guinea-pigs were made to breathe in a mixture of oxygen and hydrogen, nitrogen was given off, and that in a quantity exceeding the volume of the whole body of the animal. The lower animals also, especially insects, are said to exhale

nitrogen (Treviranus, xxxii. p. 330), and fishes to absorb it from the water in which they breathe, though they do not absorb hydrogen (Humboldt, xxxii. p. 330).

But we cannot, from these facts, safely conclude what is the case in the ordinary conditions of life. In the earlier experiments, it seemed as if small quantities of nitrogen were sometimes absorbed, and sometimes exhaled, in respiration in atmospheric air. The experiments of M. Boussingault (xviii. 1846) on turtle-doves would prove that, besides the nitrogen excreted from the digestive canal and kidneys, nearly $2\frac{1}{2}$ grains are daily discharged from the skin and lungs; and those of MM. Regnault and Reiset (xviii. 1848, and liii. 1849) on dogs, rabbits, and fowls, prove constantly a certain exhalation of nitrogen, the proportion seeming to vary according to the nature of the food, while they also find that during prolonged fasting, nitrogen, instead of being exhaled, is absorbed.

4. *Watery Vapour* is, under ordinary circumstances, always exhaled from the lungs in breathing. The quantity emitted is, as a general rule, sufficient to saturate the expired air (Valentin, iv. Bd. i. p. 547), or very nearly so (Moleschott, cxxi). Its absolute amount is, therefore, influenced by the following circumstances. First, by the volume of air expired; for the greater this is, the greater also will be the quantity of moisture exhaled. Secondly, by the quantity of watery vapour contained in the air previous to its being inspired; because the greater this is, the less will be the amount required to complete the saturation of the air. Thirdly, by the temperature of the expired air: for the higher this is, the greater will be the quantity of watery vapour required to saturate the air. Fourthly, by the length of time which each volume of inspired air is allowed to remain in the lungs; for it seems probable that, although during ordinary respiration the expired air is always saturated with watery vapour, yet when respiration is performed very rapidly the air has scarcely time to be raised

to the highest temperature, or be fully charged with moisture ere it is expelled.

For ordinary cases, however, it may be held that the expired air is saturated with watery vapour, and hence is derivable a means of estimating the quantity exhaled in any given time: namely, by subtracting the quantity contained in the air inspired from the quantity which (at the same barometric pressure) would saturate the same air at the temperature of expiration, which is ordinarily about 99°. And, on the other hand, if the quantity of watery vapour in the expired air be estimated, the quantity of air itself may from it be determined, being as much as that quantity of watery vapour would saturate at the ascertained temperature and barometric pressure.

The quantity of water exhaled from the lungs in twenty-four hours ranges (according to the various modifying circumstances already mentioned) from about 3,000 to 13,000 grains (6 to 27 ounces). Some of this is probably formed by the combination of the excess of oxygen absorbed in the lungs with the hydrogen of the blood; but the far larger proportion of it must be the mere exhalation of the water of the blood, taking place from the surfaces of the air-passages and cells, as it does from the free surfaces of all moist animal membranes, particularly at the high temperature of warm-blooded animals. It is exhaled from the lungs whatever be the gas respired, continuing to be expelled even in hydrogen gas.

Carbonic acid and water are, however, not the only principles given off from the lungs. The Rev. J. B. Reade shewed, some years ago, and Dr. Richardson's experiments confirm the fact, that ammonia is among the ordinary constituents of expired air. And very recently (cxc. 1859, p. 155) Wiederhold has stated, that not only ammonia but chloride of sodium, and even uric acid and urate of soda and ammonia, may be readily detected in the condensed vapour of expired air. His experiments, therefore, seem to prove that

the lungs may furnish a channel for the excretion of some of the same kind of solid principles as are met with in the secretion of the skin and kidneys.

### *Changes produced in the Blood by Respiration.*

The most obvious change which the blood undergoes in its passage through the lungs is that of *colour*, the dark crimson of venous blood being exchanged for the bright scarlet of arterial blood. The circumstances which have been supposed to give rise to this change, the conditions capable of effecting it independent of respiration, and some other differences between arterial and venous blood, were discussed in the chapter on BLOOD (page 56). The change in colour is, indeed, the most striking, and may appear the most important, which the blood undergoes in its passage through the lungs; yet, perhaps, its importance is very little, except so far as it is an indication of other and essential alterations effected in the composition of the blood. Of these alterations the principal are, 1st, that the blood, after passing through the lungs, is 1° or 2° warmer than it was before; 2nd, that it coagulates sooner and more firmly, and contains, apparently, more fibrine; 3rd, that it contains more oxygen, less carbonic acid, and less nitrogen.

The difference last named is, probably, the most important. It might be assumed, from what has been said of the changes in the inspired air, and it is proved, at least in regard to the first two gases, by examination of the blood itself.

The existence of carbonic acid in both arterial and venous blood has been proved by several experimenters, who have obtained appreciable quantities of it by exposing the blood to the vacuum of the air-pump, or, more certainly, by agitating it with atmospheric air, oxygen, or other gases, such as hydrogen or nitrogen. By the latter process, carbonic acid may always be extracted from venous blood. Some, indeed, have

failed to procure any gas from blood by means of the air-pump; but this may be explained by the fact observed by Magnus, that carbonic acid is not given out until the air in which the blood is placed is so rarefied that it supports only one inch of mercury. Heat, also, commonly fails to evolve carbonic acid from blood; probably because, as also observed by Magnus, a temperature high enough to set free this gas coagulates the albumen of the blood, and if albumen, impregnated with carbonic acid, is once coagulated, the gas cannot be separated from it again by means of heat.

The uncertainty of former experiments was corrected by the subsequent researches of Magnus (xvii. 1845), from which it appears sure that carbonic acid, oxygen, and nitrogen exist, both in arterial and venous blood. Their relative proportions differ in the two kinds of blood. The quantity of oxygen contained in arterial blood is twice as great as that in venous blood: being equal to from 10 to 10½ per cent. of the volume of the former, and only about 5 per cent. of the volume of the latter. The quantity of carbonic acid, on the other hand, is less in arterial than in venous blood, amounting to about 20 volumes per cent. in the former, and 25 per cent. in the latter. The quantity of nitrogen contained in the blood varies from about 1·7 to 3·3 per cent.: its relative proportion in arterial and in venous blood does not appear to differ much; but from its being commonly exhaled in small quantity from the lungs, it may be believed to be greater in the venous blood.

These facts are supported by those already mentioned, concerning the exhalation of nitrogen by animals breathing in oxygen and hydrogen, and of carbonic acid by frogs breathing in nitrogen. The gases could not be so exhaled did they not exist in solution in the blood. And there can therefore be little doubt which of the proposed *theories of respiration* should be chosen for the explanation of the process. Till the existence of the gases in the blood was clearly proved, the

theory most favoured was, that the oxygen of the atmospheric air permeates the membranous walls of the air-cells, enters the blood, and there at once combines with carbon derived from the disintegrated tissues, to form carbonic acid, which escapes, together with the greater part of the nitrogen previously absorbed from the atmosphere. It could be well objected, even when the existence of gases in the blood was doubtful, that if this theory were true, the lungs ought to be much warmer than other parts of the body, through the quantity of heat given out in the quick union of the carbon with the oxygen of the atmosphere; and that such was not found to be the case: the temperature of blood in the left side of the heart being never more than one or two degrees higher than that in the right.

Lagrange and Hassenfratz (xxxii. p. 350), impressed with this and other objections, proposed the theory, which, with some modifications, has been more recently advocated by Magnus and others, and has been shewn by them to be sufficient for the explanation of most of the phenomena yet observed in this part of the respiratory process. According to this theory, the oxygen absorbed into the blood from the atmospheric air in the lungs, is in part dissolved, and probably, also, in part loosely combined chemically with one or other of its ingredients. In this condition, the oxygen is carried in the arterial blood to the various parts of the body, and with it, is, in the capillary system of vessels, brought into near relation or contact with the elementary parts of the tissues. Herein, co-operating probably in the process of nutrition, or the removal of disintegrated parts of the tissues, about one-half of the oxygen which the arterial blood contains disappears, and a proportionate quantity of carbonic acid and water is formed. The venous blood, containing the new formed carbonic acid, returns to the lungs, where a portion of the carbonic acid is exhaled, and a fresh supply of oxygen is again taken in.

Whether part, or the whole of the oxygen absorbed during

respiration is at once united chemically with any of the constituents of the blood has not been positively determined. Among the most recent experiments on the subject are some by Ferret (lix. 1859, p. 154), which seem to prove that the principal part of the oxygen absorbed at the lungs is taken up by the red corpuscles, which appear to have a special affinity for it. It does not appear, however, to unite chemically with them, but to be held in solution; for it is readily given up when the blood is exposed to the air-pump, or when some other gas is transmitted through it. The experiments of Meyer and W. Müller (*ib.*) support the view, that the corpuscles are the constituents of the blood for which the oxygen has especial affinity. In their opinion, however, there is a direct chemical union between them and the oxygen. All these observers agree, that the corpuscles have no affinity for carbonic acid, which appears to be simply in a state of solution in the fluid part of the blood.

Although the great bulk of the oxygen absorbed by the lungs is no doubt conveyed, either in solution or slight chemical union, to the capillary system, to be there, as well as in the general course of circulation, combined with the elements of disintegrated tissues and of food, yet there is reason to believe, that a portion of it enters at once into chemical union with some of the organic constituents of the blood, and produces part of the carbonic acid exhaled in expiration, and accounts for the increase in temperature which the blood evidently undergoes in its transit through the lungs. (See Harley cxxiii. 1856, p. 78; and Savory ccxx.)

### *Influence of the Nervous System in Respiration.*

The respiratory functions are, in two respects, subject to the influence of the nervous system: namely, 1st, in the movements for the introduction and exit of air; and, 2ndly, in the interchange of the gases. These will be more particularly

considered in the sections on the MEDULLA OBLONGATA and PNEUMOGASTRIC NERVES. It may suffice to state here, that the respiratory movements, and their regular rhythm, so far as they are involuntary and independent of consciousness (as in all ordinary occasions they are), seem to be under the absolute governance of the medulla oblongata, which, as a nervous centre, receives the impression of the "necessity of breathing," and reflects it to the phrenic and such other motor nerves as will bring into co-ordinate and adapted action, the muscles necessary to inspiration.

But the respiratory movements may be voluntarily performed or variously directed; and the mind may be conscious of the necessity of breathing, either when it attends to the sensations to which that necessity gives rise, or when those sensations are more than commonly intense. In these cases, we may believe that the brain, as well as the medulla oblongata, is engaged in the process; for we have no evidence of the mind exercising either perception or will through any other organ than the brain. But even when the brain is thus in action, it appears to be the medulla oblongata, which combines the several respiratory muscles to act together. In such acts, for example, as those of coughing and sneezing, the mind must first perceive the irritation at the larynx or nose, and exercise a certain degree of will in determining the actions, as *e. g.*, in the taking of the deep inspiration that always precedes them. But the mode in which the acts are performed, and the combination of muscles to effect them, are determined by the medulla oblongata, independent of the will, and have the peculiar character of reflex involuntary movements, in being always, and without practice or experience, precisely adapted to the end or purpose.

In these and in all the other extraordinary respiratory actions, such as are seen in dyspnœa, or in straining, yawning, hiccough, and others, the medulla oblongata brings into adapted combination of action many other muscles besides those commonly exerted in respiration. Almost all the muscles

of the body, in violent efforts of dyspnœa, coughing and the like, may be brought into action at once, or in quick succession; but, more particularly, the muscles of the larynx, face, scapula, spine, and abdomen, co-operate in these efforts with the muscles of the chest. These, therefore, are often classed as secondary muscles of respiration; and the nerves supplying them, including especially the facial, pneumogastric, spinal accessory, and external respiratory nerves, were classed by Sir Charles Bell with the phrenic, as the respiratory system of nerves. There appears, however, no propriety in making a separate system of these nerves, since their mode of action is not peculiar, and many besides them co-operate in the respiratory acts. That which is peculiar in the nervous influence, directing the extraordinary movements of respiration is, that so many nerves are combined towards one purpose by the power of a distinct nervous centre, the medulla oblongata. In other than respiratory movements, these nerves may act singly or together, without the medulla oblongata; but, after it is destroyed, no movement adapted to respiration can be performed by any of the muscles, even though the part of the spinal cord from which they arise be perfect. The phrenic nerves, for example, are unable to excite respiratory movements of the diaphragm, when their connection with the medulla oblongata is cut off, though their connection with the spinal cord may be uninjured.

The influence exercised through the pneumogastric nerves upon the functions of the lungs, cannot be considered separately from their relation to the muscles of the larynx, and must therefore be deferred to the section particularly treating of the nerves.

### *Effects of the Suspension and Arrest of Respiration.*

These deserve some consideration, because of the illustration which they afford of the nature of the normal processes of

respiration and circulation. When the process of respiration is stopped, either by arresting the respiratory movements, or permitting them to continue in an atmosphere deprived of uncombined oxygen, the circulation of blood through the lungs is retarded, and at length stopped. The immediate effect of such retarded circulation is an obstruction to the exit of blood from the right ventricle: this is followed by delay in the return of venous blood to the heart; and to this succeeds venous congestion of the nervous centres and all the other organs of the body. In such retardation, also, an unusually small supply of blood is transmitted through the lungs to the left side of the heart; and this small quantity is venous.

The condition then, in which a suffocated, or asphyxiated, animal dies is, commonly, that the left side of the heart is nearly empty, while the lungs, right side of the heart, and other organs, are gorged with venous blood. To this condition many things contribute. 1st. The obstructed passage of blood through the lungs, which appears to be the first of the events leading to suffocation, seems to depend on the cessation of the interchange of gases, as if blood charged with carbonic acid could not pass freely through the pulmonary capillaries. That such may be the case, is shown by Mr. Wharton Jones's observation, that the circulation in the web of the frog's foot may be retarded or arrested by directing on the web a stream of carbonic acid, under the influence of which the blood-corpuscles appear to cluster and stagnate in the vessels. But the stagnation of blood in the pulmonary capillaries would not, perhaps, be enough to stop entirely the circulation, unless the actions of the heart were also weakened; for Mr. Erichsen (xciv. vol. lxiii. p. 22), having pithed dogs, and tied the right bronchus, and maintained artificial respiration in the left lung, found that, so long as the heart's action continued, black blood still flowed through a right pulmonary vein, though far less freely than red blood through a left one.

Therefore, 2ndly, the fatal result is due, in some measure,

to the weakened action of the right side of the heart, in consequence, probably, of its over-distension by blood continually flowing into it, this flow, probably, being much increased by the powerful but fruitless efforts continually made at inspiration (Eccles, lxxi. vol. xliv. p. 657).

Thirdly, because of the obstruction at the right side of the heart, there must be venous congestion in the medulla oblongata and nervous centres: and this evil is augmented by the left ventricle receiving and propelling none but venous blood. Hence, slowness and disorder of the respiratory movements and of the movements of the heart may be added. But this alone does not explain asphyxia; for Mr. Erichsen found that a dog was asphyxiated in the ordinary time, although arterial blood was made to circulate through the nervous centres during the whole time. However, under all these conditions combined, the heart at length ceases to act. The time at which the complete cessation ensues is uncertain. The domestic Mammalia usually perish, after submersion in water, in about three minutes: there are exceptional cases, in which animals and human beings have been revived after being under water for a longer period. According to Mr. Erichsen, (l. c. p. 30), in dogs suffocated by drowning, the voluntary movement ceases in $1\frac{3}{4}$ minutes; the involuntary in $2\frac{1}{2}$ after submersion; the ventricular contractions continue for a period ranging from $6\frac{1}{2}$ to 14 minutes, the average time being $9\frac{1}{2}$ minutes; and the blood in the arteries becomes as black as that in the veins in about $1\frac{1}{2}$ minutes. In the human subject, he thinks that the ventricular contractions always cease at or before the expiration of five minutes after complete submersion; for persons are rarely, if ever, saved if they have been under water more than four minutes. The instances in which recovery has taken place after a longer immersion, are probably to be explained by the occurrence of fainting at the moment of the accident; for with the circulation enfeebled, the deprivation of air may be endured much longer than it

can be while the blood still circulates quickly and accumulates carbonic acid.

It is to the accumulation of carbonic acid in the blood, and its conveyance into the organs that we must, in the first place, ascribe the phenomena of asphyxia. For when this does not happen, all the other conditions may exist without injury; as they do, for example, in hybernating, warm-blooded animals. In these, life is supported for many months in atmospheres in which the same animals, in their full activity, would be speedily suffocated. During the periods of complete torpor, their respiration almost entirely ceases; the heart acts very slowly and feebly; the processes of organic life are all but suspended, and the animal may be with impunity completely deprived of atmospheric air. Spallanzani kept a marmot, in this torpid state, immersed for four hours in carbonic acid gas, without its suffering any apparent inconvenience. Dr. Marshall Hall kept a lethargic bat under water for sixteen minutes, and a lethargic hedgehog for 22½ minutes; and neither of the animals appeared injured by the experiment (lxxiii. vol. ii. p. 771).

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## CHAPTER VII.

### ANIMAL HEAT.

INTIMATELY associated with the process of respiration are the production of animal heat, and the maintenance of a uniform temperature of the body; conditions as essential to the continuance of life in warm-blooded animals, as the extrication of carbonic acid and the absorption of oxygen are.

*The average temperature of the human body*, in those internal parts which are most easily accessible, such as the mouth and

rectum, may be estimated at from 98° to 103° F. Brown-Séquard fixes the standard at 103° F. In children, the temperature is commonly as high as 102° F. In old persons, it is about the same as in adults (Davy, xliii. 1844). Of the external parts of the body, the temperature becomes lower the further they are removed from the centre of the body; thus, in the human subject, a thermometer placed in the axilla was found by Dr. John Davy to stand at 98° F., at the loins it indicated a temperature of 96½°, on the thigh 94°, on the leg 93° or 91°, on the sole of the foot 90° (xliii. 1844). In disease, the temperature of the body may deviate, by several degrees above and below, from the average of health. In some diseases, as scarlatina and typhus, it rises as high as 106° or 107° F.; and in children, M. Roger has observed the temperature of the skin to be raised to 108·5° Fah. (cxxii. 1844). In the *morbus cæruleus*, in which there is defective arterialization of the blood from malformation of the heart, the temperature of the body is often as low as 79° or 77½°; in Asiatic cholera a thermometer placed in the mouth, sometimes rises only to 77° or 79°. M. Roger observed the temperature of the body in children to be sometimes reduced in disease to 74·3°.

The temperature of the body in health, is about 1½° F. lower during sleep than while awake. According to Dr. Davy (cxxiii. June 1845) it is highest in the morning after rising from sleep, continues high but fluctuating till evening, and is lowest about midnight. Sustained mental exertion elevates it slightly; continued bodily exercise does so to a considerable extent; after feeding, also, it is somewhat raised. All these facts are important, both as showing variations in the temperature of the body, correspondent with those in the production of carbonic acid in the same circumstances, and as proving that the influence which slight changes in the organic economy of warm-blooded animals have, is as great or greater than that exercised by even extreme variation in the external temperature which they are exposed. For in warm climates, Dr. Davy found the temperature of the interior of the body only from

2·7° to 3·6° F. higher than in temperate climates; and during the voyage of the "Bonite," the French naturalists, who had an opportunity of observing the influence of various climates on the same persons, found that the temperature of the human body rises and falls in only a slight degree, even in extremes of external temperature; that it falls slowly in passing from hot to cold climates, and rises more rapidly in returning towards the torrid zone: but that these changes in the temperature of the body, are more considerable in some individuals than in others (xviii. 1838, p. 456).

The temperature maintained by Mammalia in an active state of life, according to the tables of Tiedemann and Rudolphi, averages 101°. The extremes recorded by them were 96° and 106°, the former in the narwhal, the latter in a bat (Vespertilio Pipistrella). In birds, the average is as high as 107°; the highest temperature, 111·25°, being in the small species, the linnets, etc. (cxxv. p. 234). Among reptiles, Dr. John Davy found, that while the medium they were in was 75°, their average temperature was 82·5°. As a general rule, their temperature, though it falls with that of the surrounding medium, is, in temperate media, two or more degrees higher; and though it rises also with that of the medium, yet at very high degrees it ceases to do so, and remains even lower than that of the medium. Fish, insects, and other Invertebrata present as a general rule, the same temperature as the medium in which they live, whether that be high or low; only among fish, the tunny-tribe, with strong hearts, and red meat-like muscles, and more blood than the average of fish have, are generally 7° warmer than the water around them.

The difference, therefore, between what are commonly called the warm- and the cold-blooded animals, is not one of absolutely higher or lower temperature; for the animals which to us, in a temperate climate, feel cold (being like the air or water, colder than the surface of our bodies), would, in an external

temperature of 100° or 200°,* have nearly the same temperature, and feel hot to us. The real difference is, as Mr, Hunter expressed it (i. vol. iii. p. 16, and vol. iv. p. 131, et seq.), that what we call warm-blooded animals (birds and Mammalia), have a certain "permanent heat in all atmospheres," while the temperature of the others, which we call cold-blooded, is "variable with every atmosphere."

The power of maintaining a uniform temperature, which Mammalia and birds possess, is combined with the want of power to endure such changes of temperature as are harmless to the other classes; and when their power of resisting change of temperature ceases, they suffer serious disturbances or die. M. Magendie has shewn that birds and rabbits die when, being exposed to great external heat, their temperature is raised as much as 9° above the natural standard: but they bear a reduction of the temperature of the interior of the body to a much greater amount before very dangerous or fatal consequences ensue (cxciii. 1850).

In all the ordinary circumstances of life, the maintenance of uniform temperature is effected by the production of heat sufficient to compensate for that which is constantly lost in radiation into the medium in which we live, or in combination with the fluids evaporating from the exposed surfaces of the body.

The losses thus sustained are extremely various in different circumstances; and the degrees of power which animals possess of adapting themselves to such differences are equally various. Some live best in cold regions, where they produce abundant heat for radiation, and cannot endure the heat of warm climates, where the heat that they habitually produce would, probably, be excessive, and by its continual, though perhaps small excess, would generate disease; others, naturally inha-

* Humboldt and Bonpland saw fish thrown up from volcanoes alive, and apparently in health, along with water and vapour which raised the thermometer to 210°.

biting warm climates, die if removed to cold ones, as if because their power of producing heat were not quite sufficient to compensate for the constantly larger abstraction of it by radiation. Man, with the aid of intellect for the provision of artificial clothing, and with command over food, is, in these respects, superior to all other creatures; possessing the greatest power of adaptation to external temperature, and being capable of enduring extreme degrees of heat as well as of cold without injury to health. His power of adaptation is sufficient for the maintenance of a uniform temperature in a range of upwards of 200° Fahrenheit; a power which is only shared by some of the domestic animals who are his companions in his various abodes.

### *Sources and Mode of Production of Heat in the Body.*

To explain the production of heat in the body, several theories have been advanced; but it now appears almost certain that the correct one is that which refers the generation of heat, primarily and in general, to certain chemical processes going on in the system; but admits, at the same time, that as these chemical changes are carried on in parts whose functions are, to a certain extent, under the influence of the nervous system, therefore the production of heat is liable to be modified, either locally or in every part, by the operation of that system.

In explaining the chemical changes effected in the process of respiration (p. 170), it was stated that the oxygen of the atmosphere taken into the blood is, most probably, combined partly in the lungs, partly in the course of the circulation, but mainly in the systemic capillary vessels, with the carbon and the hydrogen of disintegrated and absorbed tissues, and certain elements of food which have not been converted into tissues. That such a combination, between the oxygen of the atmosphere and the carbon and hydrogen in the blood, is con-

tinually taking place, is made nearly certain by the fact, that a larger amount of carbon and hydrogen is constantly being added to the blood from the food, than is required for the ordinary purposes of nutrition, and that a quantity of oxygen is also constantly being absorbed from the air in the lungs, of the disposal of which no account can be given except by regarding it as combining, for the most part, with the excess of carbon and hydrogen, and being evaporated in the form of carbonic acid and water. In other words, the blood of warm-blooded animals appears to be always receiving from the digestive canal and the lungs more carbon, hydrogen, and oxygen, than are consumed in the repair of the tissues; and to be always emitting carbonic acid and water, for which no other source can be ascribed than the combination of these elements. In the processes of such combination, heat must be continually produced in the animal body. The same amount of heat will be evolved in the union of any given quantities of carbon and oxygen, and of hydrogen and oxygen, whether the combination be rapid and evident, as in ordinary combustion, or slow and imperceptible as in the changes which are believed to occur in the living body. And since the heat thus arising will be generated wherever the blood is carried, every part of the body will be heated equally; or so nearly equally that the rapid circulation of the blood will quickly remove any diversities of temperature in different parts.

To establish this theory, it needs to be shewn, that the quantity of carbon and hydrogen which, in a given time, unites in the body with oxygen, is sufficient to account for the amount of heat generated in the animal within the same time: an amount capable of maintaining the temperature of the body at from 98° to 100°, notwithstanding a large loss by radiation and evaporation.*

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* Some heat will also be generated in the combination of sulphur and phosphorus with oxygen, to which reference has been made (p. 152);

An attempt to determine this point was made by Dulong and Despretz. Dulong introduced different mammiferous animals, carnivorous as well as herbivorous, into a receiver, in which the changes produced in the air by respiration, and the volume of the different products, could be determined at the same time that the amount of heat lost by the animal could be ascertained. His experiments led him to conclude, among other points, that supposing all the oxygen, absorbed into the blood from the air in the lungs, were combined with carbon and hydrogen in the system, and that as much heat were thus generated as would be developed during the quick combustion of equal quantities of oxygen and carbon, and of oxygen and hydrogen, still, the whole quantity of heat produced would amount to only from $\frac{3}{4}$ to $\frac{4}{5}$ of that which is developed during the same space of time by carnivorous as well as herbivorous animals. Despretz placed animals in a vessel surrounded with water; an uninterrupted current of air to and from the vessel was maintained, and the volume and composition of the air employed were ascertained both before and after the experiment (which was continued $1\frac{1}{2}$ or 2 hours), as well as the increase in the temperature of the surrounding water during its progress: by this means it was found that the heat which should have been generated, according to the chemical theory of respiration, would account for from 0·76 to 0·91 only of that which the animals really gave out during the same time. The failing of these experiments to account for all the heat produced threw doubts on the chemical theory of animal heat (as the proposed explanation has been called), till Liebig shewed that Dulong and Despretz were in error in their conclusions, from having formed too low an estimate of the heat produced in the combustion of carbon and hydrogen. On repeating their

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but the amount thus produced has not been estimated, and need not be considered in the exposition of a theory which can, at present, be stated in only the most general terms.

experiments, and using the more accurate numbers to represent these *combustion-heats*, Liebig found reason to believe that the quantity of heat which would be generated, by the union of the oxygen absorbed into the blood from the atmosphere with the carbon and hydrogen taken into the system as food, would be sufficient to account for the whole of the caloric formed in the animal body.*

Many things observed in the economy and habits of animals are explicable by this theory, and are, therefore, evidence for its truth. Thus, as a general rule, in the various classes of animals, as well as in individual examples of each class, the quantity of heat generated in the body is in direct proportion to the activity of the respiratory process. The highest animal temperature, for example, is found in birds, in whom the function of respiration is most actively performed. In Mammalia, the process of respiration is less active, and the average temperature of the body less, than in birds. In reptiles, both the respiration and the heat are at a much lower standard; whilst in animals below them, in which the function of respiration is at the lowest point, a power of producing heat is, in ordinary circumstances, hardly discernible. Among these lower animals, however, the observations of Mr. Newport (xliii. 1837) supply confirmatory evidence. He shews that the larva, in which the respiratory organs are smaller in comparison with the size of the body, has a lower temperature than the perfect insect. Volant insects have the highest temperature, and they have always the largest respiratory organs and breathe the greatest quantity of air; while among terrestrial insects, those also produce the most heat which have the largest respiratory organs and breathe the most air. During sleep, hybernation, and other states of inaction, respiration is slower or suspended, and the temperature is proportionably diminished; while on the other hand, when

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* Liebig's estimates and calculations may be referred to in the "Lancet" (Feb. 1845).

the insect is most active and respiring most voluminously, its amount of temperature is at its maximum, and corresponds with the quantity of respiration. Neither the rapidity of the circulation, nor the size of the nervous system, according to Mr. Newport, presents such a constant relation to the evolution of heat.

Similar evidence in favour of this theory of animal heat is furnished by the fact that heat is sometimes evolved by plants, in a quantity which appears to be in direct proportion to the amount of oxygen they at the same time absorb and convert into carbonic acid. For example, their evolution of heat is most evident during flowering and the germination of seeds, the times at which the largest amount of carbonic acid is exhaled.

The quantity and quality of food consumed by man and animals in the different climates and seasons, also appear to be adapted to the production of various amounts of heat by the combination of carbon and hydrogen with oxygen. In northern regions, for example, and in the colder seasons of more southern climes, the quantity of food consumed is (speaking very generally) greater than is consumed by the same men or animals in opposite conditions of climate and seasons. And the food which appears naturally adapted to the inhabitants of the coldest climates, such as the several fatty and oily substances, abounds in carbon and hydrogen, and is fitted to combine with the large quantities of oxygen which, breathing cold dense air, they absorb from their lungs.

The *influence of the nervous system* in modifying the production of heat has been already referred to. The experiments and observations which best illustrate it are those showing first, that when the supply of nervous influence to a part is cut off, the temperature of that part falls below its ordinary degree; and, secondly, that when death is caused by severe injury to, or removal of the nervous centres, the temperature of the body rapidly falls, even though artificial respiration be

performed, the circulation maintained, and to all appearance the ordinary chemical changes of the body be completely effected. It has been repeatedly noticed, that after division of the nerves of a limb, its temperature falls: and this diminution of heat has been remarked still more plainly in limbs deprived of nervous influence by paralysis. For example, Mr. Earle (xli. vol. vii. p. 173) found the temperature of the hand of a paralysed arm to be 70°, while the hand of the sound side had a temperature of 92° F. On electrifying the paralysed limb, the temperature rose to 77°. In another case, the temperature of the paralysed finger was 56° F., while that of the unaffected hand was 62°. Sir B. C. Brodie (xliii. 1811 and 1812) found, that if artificial respiration was kept up in animals killed by decapitation, division of the medulla oblongata, destruction of the brain, or poisoning with Worara poison, the action of the heart continued, and the blood underwent the usual changes in the lungs, as shewn by the analysis of the air respired, but that the heat of the body was not maintained: on the contrary, being cooled by the air forced into the lungs, it became cold more rapidly than the body of an animal in which artificial respiration was not kept up. With equal certainty, though less definitely, the influence of the nervous system on the production of heat is shewn in the rapid and momentary increase of temperature, sometimes general, at other times quite local, which is observed in states of nervous excitement; in the general increase of warmth of the body, sometimes amounting to perspiration, which is excited by passions of the mind; in the sudden rush of heat to the face, which is not a mere sensation; and in the equally rapid diminution of temperature in the depressing passions. But none of these instances suffices to prove that heat is generated by mere nervous action, independent of any chemical change; all are as well explicable on the supposition that the influence of the nervous system alters, in some way, the chemical processes from which the heat is commonly generated. There are ample proofs that the nervous system, especially in the most

highly organised animals, does so modify all the functions of organic life; and it appears more reasonable to suppose that it thus influences the production of heat, than to ascribe to it any more direct agency.

The temporary increase of heat in a part, as in the instances mentioned above, is no doubt in great measure due to a larger afflux of blood to the part, in consequence of temporary relaxation of the walls of the small arteries through nervous agency. M. Bernard, for example, found that when he divided, on one side of the neck, the trunk which unites the sympathetic ganglia, or when he removed the superior cervical ganglion, an increase of temperature at once took place on the corresponding side of the face, and continued for many months (ccvii. p. 418). This observation has since been abundantly confirmed. It will be more fully considered when speaking of the physiology of the sympathetic nerve.

In the foregoing pages, the illustrations of the power of maintaining an uniform temperature have had reference to the ordinary case of man living in a medium colder than his body, and therefore losing heat both by radiation and evaporation. The losses in these two ways will bear, in general, an inverse proportion to one another; the small loss of heat by evaporation in cold climates may go far to compensate for the greater loss by radiation; as, on the other hand, the great amount of fluid evaporated in hot air may remove nearly as much heat as is commonly lost by both radiation and evaporation in ordinary temperatures. Thus, it is possible, that the quantities of heat required for the maintenance of an uniform proper temperature in various climates and seasons are not so different as they may, at first thought, seem: but on these points no accurate information has yet been obtained.*

Neither, as to the maintenance of the temperature of the

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* Vierordt has made estimates of the heat given out, per minute, from the lungs in warming the inspired air, and in combination with the evaporated water; it would be enough to heat (at the most) 96·34 grains

body in hot air is much more known than that great heat can for a time be borne with little change in the proper temperature of the body, provided the air be dry. Sir Charles Blagden and others supported a temperature varying between 198° and 211° F. in dry air for several minutes; and in a subsequent experiment he remained eight minutes in a temperature of 260°. Delaroche and Berger (cxxxii.) observed that the temperature of rabbits was raised only a few degrees when they were exposed to heat varying from 122° to 194°. But such heats are not tolerable when the air is moist as well as hot, so as to prevent evaporation from the body. M. C. James (xix. April, 1844) states, that in the vapour baths of Nero he was almost suffocated in a temperature of 112°, while in the caves of Testaccio, in which the air is dry, he was but little incommoded by a temperature of 176°. In the former, evaporation from the skin was impossible; in the latter, it was, probably, abundant, and the layer of vapour which would rise from all the surface of the body would, by its very slowly conducting power, defend it for a time from the full action of the external heat.

It remains to notice certain conditions by which the production of heat is modified.

The *effects of age* are noticeable. M. Edwards found the power of generating heat to be less in old people: and the same was observed by Dr. Davy (xliii. 1844), who, in eight people, between eighty-seven and ninety-five years old, found that, although the average temperature of the body was not lower than that of younger persons, yet the power of resisting cold was less in them—exposure to a low temperature causing a greater reduction of heat than in young persons.

The same rapid diminution of temperature was observed by

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of water from 32° to 212° (cx. p. 236). At this rate, the loss by evaporation from the skin and lungs together may be roughly estimated at enough to heat nearly 4000 grains of water from 32° to 212°.

M. Edwards in the new-born young of most carnivorous and rodent animals when they were removed from the parent, the temperature of the atmosphere being between 50° and 53½° F.; whereas, while lying close to the body of the mother, their temperature was only 2 or 3 degrees lower than hers. The same law applies to the young of birds. Young sparrows, a week after they were hatched, had a temperature of 95° to 97°, while in the nest; but when taken from it, their temperature fell in one hour to 66½°, the temperature of the atmosphere being at the time 62½°. It appears from his investigations, that in respect of the power of generating heat, some Mammalia are born in a less developed condition than others; and that the young of dogs, cats, and rabbits, for example, are inferior to the young of those animals which are not born blind. The need of external warmth to keep up the temperature of new-born children is well known; the researches of M. Edwards show, that the want of it is, as Hunter suggested, a much more frequent cause of death in new-born children than is generally supposed, and furnish a strong argument against the idea, that children, by early exposure to cold, can soon be hardened into resisting its injurious influence.

*Active exercise,* as already stated, raises the temperature of the body. This may be partly ascribed to the fact, that every muscular contraction is attended by the development of one or two degrees of heat in the acting muscle; and that the heat is increased according to the number and rapidity of these contractions, and may be quickly diffused by the blood circulating from the heated muscles. Possibly also, some heat may be generated in the various movements, stretchings, and recoilings of the other tissues, as the arteries, whose elastic walls, alternately dilated and contracted, may give out some heat, just as caoutchouc alternately stretched and recoiling becomes hot. But the heat thus developed cannot be so much as some have supposed (Winn, xvii. Ser. 3, vol. xiv. p. 174; Winter, xxx. 1843, p. 794).

The *influence of external coverings* for the body must not be unnoticed. In warm-blooded animals, they are always adapted, among other purposes, to the maintenance of uniform temperature; and man adapts for himself such as are, for the same purpose, fitted to the various climates to which he is exposed. By their means, and by his command over food and fire, perhaps as much as by his capacity of developing appropriate amounts of heat, he maintains his temperature on all accessible parts of the surface of the earth.

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## CHAPTER VIII.

### DIGESTION.

DIGESTION is the process by which those parts of our food which may be employed in the formation and repair of the tissues, or in the production of heat, are made fit to be absorbed and added to the blood.

Food may be considered in its relation to the two purposes above-mentioned; and the various articles of food may be artificially classified according as they are chiefly subservient to one or the other of these purposes. All articles of food that are to be employed in the production of heat, contain a large amount of carbon and hydrogen; and of those which are appropriate for the maintenance of the several tissues (except the adipose) nearly all are characterised by the possession of nitrogen, and are capable of ready conversion into the nitrogenous principles of the blood.

The name of *nutritive* or *plastic* is given to those principles of food which admit of conversion into the albumen or fibrine

of the blood, and of being subsequently assimilated, through the medium of the blood, by the tissues. And those principles, comprising the greater part of the non-nitrogenous materials of food, in the form of fat, starch, sugar, gum, and other similar substances, which are believed to be employed in the production of heat, are named *calorifacient*, or sometimes *respiratory* food.

An easier division of foods than this according to their destination is derived from their origins; for all consist of either animal or vegetable substances. No substance can afford nutriment, even though it contain all the elements of organic bodies, unless it have all the natural peculiarities of organic composition, and contain, incorporated with its other elements, some of those derived from the mineral kingdom, which, as before mentioned (p. 3), are found in the organized tissues; such as sulphur, iron, lime, magnesia, etc.

Man is supported as well by food constituted wholly of animal substances, as by that which is formed entirely of vegetable matters; and the structure of his teeth, as well as experience, seems to point out that he is destined for a mixed kind of aliment. In the case of carnivorous animals, the food upon which they exist, consisting as it does of the flesh and blood of other animals, not only contains all the elements of which their own blood and tissues are composed, but contains them combined, probably, in the same forms. Therefore, little more may seem requisite, in the preparation of this kind of food for the nutrition of the body, than that it should be dissolved and conveyed into the blood in a condition capable of being re-organized. But in the case of the herbivorous animals, which feed exclusively upon vegetable substances, it might seem as if there would be greater difficulty in procuring food capable of assimilation into their blood and tissues, But the chief ordinary articles of vegetable food contain substances identical, in composition, with the albumen, fibrine, and caseine, which constitute the principal nutritive materials in animal food. Albumen is abundant in the juices and seeds

of nearly all vegetables; the gluten which exists especially in corn and other seeds of grasses as well as in their juices, is identical in composition with fibrine, and is commonly named vegetable fibrine; and the substance named legumen, which is obtained especially from peas, beans, and other seeds of leguminous plants, and from the potato, is identical with the caseine of milk. All these vegetable substances are, equally with the corresponding animal principles, and in the same manner, capable of conversion into blood and tissues; and like the blood and tissues in both classes of animals, the nitrogenous food of both may be regarded as in essential respects similar.

An apparently more considerable difference between animal and vegetable foods consists in the different kinds, and proportionately larger quantity, of the non-nitrogenous principles contained in the latter. The only non-nitrogenous organic substances in animal food are furnished by the fat; and in some instances, by the vegetable matters that may chance to be in the digestive canals of such animals as are eaten whole. The amount of these is far less than that of the non-nitrogenous substances consumed by herbivorous animals, in their quantities of starch, sugar, gum, oil, and other ternary compounds. Yet, that the final destination of the ternary principles is the same in both classes, is almost proved by the ability of man and many other animals to subsist, and apparently to maintain an identical composition and an uniform temperature, with food of either kind.

Again, the several alimentary substances, from both animal and vegetable sources, may be arranged, according to the system of Dr. Prout, in three classes, under the names of *albuminous*, *saccharine*, and *oleaginous* principles. In the albuminous group are included all the nitrogenous principles, whether derived from the animal or from the vegetable kingdom. These comprise albumen, fibrine, caseine, gelatine, and chondrine; the two latter substances being classed under this head on

account of their bearing a closer resemblance to the albuminous than to any other principles of food. The *saccharine* group comprises substances derived exclusively from the vegetable kingdom, viz., sugar itself, and the various principles capable of being converted into it, as starch, gum, pectine, and lignine or woody fibre: all of which are composed of carbon, hydrogen, and oxygen, with the two latter in the proportion in which they form water. The *oleaginous* group includes the various kinds of fatty and oily principles, which occur abundantly in both animal and vegetable kingdoms. All are composed principally of carbon and hydrogen: the quantity of the former element usually exceeding that of the latter; and the quantity of the latter being more than sufficient to form water with the oxygen they contain. Besides these three principal divisions, Dr. Prout makes a fourth division for the *aqueous* part of food. For, besides that water constitutes nearly four-fifths of the total weight of the animal body, and must therefore enter largely into the composition of food, it is highly probable that it plays an important part in the various transformations undergone in the system, and thus contributes materially to the nutrition of the different textures.

It has been already said, that animals cannot subsist on any but organic substances, and that these must contain the several elements and compounds which are naturally combined with them: in other words, not even organic compounds are nutritive, unless they are supplied in their natural state. The most singular instance of this fact is, perhaps, that of the production of scurvy by the want of vegetable food, and its cure by the giving of vegetables; which however must be either raw, or simply preserved, or so cooked, that their saline constituents may not be removed from them. Pure fibrine, pure gelatine, and other principles purified from the substances naturally mingled with them, are incapable of supporting life for more than a brief time.

Moreover, health cannot be maintained by any number of

substances derived exclusively from one of the three groups of alimentary principles. A mixture of nitrogenous and non-nitrogenous substances, together with the inorganic principles which are severally contained in them, is essential to the well-being, and, generally, even to the existence of an animal. The truth of this is demonstrated by experiments performed for the purpose, and is illustrated by the composition of the food prepared by nature, as the exclusive source of nourishment to the young of Mammalia, namely milk. In milk, the albuminous group of aliments is represented by the caseine, the oleaginous by the butter, the aqueous by the water, the saccharine by the sugar of milk. Milk, likewise, contains phosphate of lime, alkaline and other salts, and a trace of iron; so that it may be briefly said to include all the substances which the tissues of the growing animal need for their nutrition, and which are required for the production of animal heat. The yelk and albumen of eggs are in the same relation as food for the embryoes of oviparous animals, as milk is to the young of Mammalia, and afford another example of mixed food being provided as the most perfect for nutrition.

The experiments illustrating the same principle have been chiefly performed by Magendie (cxxxiii.). Dogs were fed exclusively on sugar and distilled water. During the first seven or eight days they were brisk and active, and took their food and drink as usual; but in the course of the second week, they began to get thin, although their appetite continued good and they took daily between six and eight ounces of sugar. The emaciation increased during the third week, and they became feeble, and lost their activity and appetite. At the same time an ulcer formed on each cornea, followed by an escape of the humours of the eye ; this took place in repeated experiments. The animals still continued to eat three or four ounces of sugar daily; but became at length so feeble as to be incapable of motion, and died on a day varying from the 31st to the 34th. On dissection, their bodies presented all the ap-

pearances produced by death from starvation; indeed, dogs will live almost the same length of time without any food at all.

When dogs were fed exclusively on gum, results almost similar to the above ensued. When they were kept on olive-oil and water, all the phenomena produced were the same, except that no ulceration of the cornea took place : the effects were also the same with butter. Tiedemann and Gmelin obtained very similar results. They fed different geese, one with sugar and water, another with gum and water, and a third with starch and water. All gradually lost weight. The one fed with gum died on the sixteenth day; that fed with sugar on the twenty-second; the third which was fed with starch, on the twenty-fourth, and another on the twenty-seventh day; having lost, during these periods, from one-sixth to one-half of their weight. The experiments of Chossat (xix. Oct. 1843) and Letellier (xii. 1844) prove the same; and in men, the same is shown by the various diseases to which they who consume but little nitrogenous food are liable, and especially, as Dr. Budd has shown, by the affection of the cornea which is observed in Hindus feeding almost exclusively on rice. But it is not only the non-nitrogenous substances, which, taken alone, are insufficient for the maintenance of health. The experiments of the Academies of France and Amsterdam were equally conclusive that gelatine alone soon ceases to be nutritive (xxv. 1843-4, p. 35).

These facts prove the necessity of a mixture of elementary principles in the food; and beyond this, Magendie's further experiments appear to prove, that animals cannot live long if fed exclusively on any single article of food (except milk), even although it contains principles belonging to each of the three groups of alimentary substances. For example (to mention only some of his results), a dog fed on white bread and water, did not live more than fifty days; rabbits and guinea-pigs fed on any one of the following substances,—wheat, oats, barley, cabbage, or carrots,—died with all the signs of

inanition in fifteen days; while if the same substances were given simultaneously, or in succession, the animals suffered no ill effect.

### *Changes of the Food effected in the Mouth.*

The first of a series of changes to which the food is subjected in the digestive canal, takes place in the cavity of the mouth; the solid articles of food are here submitted to the action of the teeth, whereby they are divided and crushed, and, by being at the same time mixed with the fluids of the mouth, are reduced to a soft pulp, capable of being easily swallowed. The fluids with which the food is mixed in the mouth, consist of the secretion of the salivary glands, and the mucus secreted by the lining membrane of the whole buccal cavity.

The glands concerned in the production of *saliva*, are very extensive, and in man and Mammalia generally, are presented in the form of four pairs of large glands, the parotid, submaxillary, sublingual, and intralingual, and numerous smaller bodies, of similar structure and with separate ducts, which are scattered thickly beneath the mucous membrane of the lips, cheeks, soft palate, and root of the tongue. These all have the structure common to what are termed conglomerate glands, which will be spoken of in the chapter on SECRETION. Saliva, as it commonly flows from the mouth, is mixed with the secretion of the mucous membrane, and often with air bubbles, which, being retained by its viscidity, make it frothy.

When obtained from the parotid-ducts, and free from mucus, saliva is a transparent watery fluid, the specific gravity of which varies from 1·004 to 1·008, and in which, when examined with the microscope, are found floating a number of minute particles, derived from the secreting ducts and vesicles

of the glands. In the impure or mixed saliva are found, besides these particles, numerous epithelial scales separated from the surface of the mucous membrane of the mouth and tongue, and mucus-corpuscles, discharged for the most part from the tonsils, which, when the saliva is collected in a deep vessel, and left at rest, subside in the form of a white opaque matter, leaving the supernatant salivary fluid transparent and colourless or with a pale blueish-grey tint. In *reaction*, the saliva, when first secreted, appears to be always alkaline; and that from the parotid gland is said to be more strongly alkaline than that from the other salivary glands. This alkaline condition is most evident when digestion is going on, and according to Dr. Wright (xxx. 1842-3), the degree of alkalinity of the saliva bears a direct proportion to the acidity of the gastric fluid secreted at the same time. During fasting, the saliva, although secreted alkaline, shortly becomes acid; and it does so, especially when secreted slowly, and allowed to mix with the acid mucus of the mouth, by which its alkaline reaction is destroyed.

According to Dr. Wright (xxx. March, 1842), whose analysis does not materially differ from the more recent analyses of Frerichs (lix. 1850, p. 136), Jacubowitsch (ccviii. p. 7, e.s.), and others, the *composition of saliva* is—

| | | | |
|---|---|---|---|
| Water . . . . | 988·1 | Mucus . . . . | 2·6 |
| Ptyaline . . . | 1·8 | Ashes . . . . | 4·1 |
| Fatty matter . . . | ·5 | Loss . . . . | 1·2 |
| Albumen (with soda) . | 1·7 | | 1000·0 |

Ptyaline is the name given to a peculiar nitrogenous substance, which is insoluble in alcohol. By Mialhe it is stated to be closely analogous to the vegetable substance termed diastase; according to Lehmann (cciii. vol. ii. p. 15) it closely resembles both albumen and caseine, though it is not identical with either of them.

The ashes of saliva have been analysed by Enderlin (x. 1844),

who found that they consist of substances very similar to those in the ashes of blood, and he believes that the alkalinity of the saliva, like that of the blood, is due to the tribasic phosphate of soda. The other salts which he found in it were chlorides of sodium and potassium, sulphate of soda, and phosphates of lime, magnesia, and of iron. The presence of iron has been denied, but Dr. G. Harley states that he never found it absent from healthy human saliva (cxc. Jan. 1860.) Saliva also contains a small quantity of sulpho-cyanogen, in the form of sulpho-cyanide of potassium; its presence is indicated by a deep red colour when saliva is mixed with a neutral solution of a salt of the peroxide of iron. See, on this point, Pettenkofer (lix. 1846, p. 115), Strahl (lix. 1847, p. 100), and Bidder and Schmidt (ccviii. p. 10). The use of this constituent is still unknown. The tartar which collects on the human teeth consists almost entirely of the earthy phosphates, combined with about 19 per cent. of animal matter, and containing shells of infusoria, and other accidental mixtures.

*The rate at which saliva is secreted* is subject to considerable variation. When the tongue and muscles concerned in mastication are at rest, and the nerves of the mouth are subject to no unusual stimulus, the quantity secreted is not more than sufficient, with the mucus to keep the mouth moist. But the flow is much accelerated when the movements of mastication take place, and especially when they are combined with the presence of food in the mouth. It may be excited also, even when the mouth is at rest, by the mental impressions produced by the sight or thought of food; also by the introduction of food into the stomach. The influence of the latter circumstance was well shewn in a case mentioned by Dr. Gairdner, of a man whose pharynx had been divided: the injection of a meal of broth into the stomach was followed by the secretion of from six to eight ounces of saliva (Brown-Séquard, xxx. 1858).

Under these varying circumstances, the *quantity* of saliva

secreted in twenty-four hours varies also; its average amount is thought to range from fifteen to twenty ounces. In a man who had a fistulous opening of the parotid duct, Mitscherlich found that the quantity of saliva discharged from it during twenty-four hours, was from two to three ounces; and the saliva collected from the mouth during the same period, and derived from the other salivary glands, amounted to six times more than that from the one parotid. Bidder and Schmidt however, estimate the amount much higher than this, believing that the average daily excretion in man is upwards of three pounds (ccviii. p. 14; see also Bernard, ccxiv., July 7, 1860.)

The *purposes served by saliva* are of several kinds. In the first place, acting mechanically, it keeps the mouth in a due condition of moisture, facilitating the movements of the tongue in speaking, and the mastication of food. Thus also it serves in dissolving sapid substances, and rendering them capable of exciting the nerves of taste. But the principal mechanical purpose of the saliva is, that by mixing with the food during mastication, it makes it a soft pulpy mass, such as may be easily swallowed. To this purpose the saliva is adapted both by quantity and quality. For speaking generally, the quantity secreted during feeding is in direct proportion to the dryness and hardness of the food: as M. Lassaigne has shewn, by a table of the quantity produced in the mastication of a hundred parts of each of several kinds of food; thirty parts suffice for a hundred parts of crumb of bread; but not less than 120 for the crusts; 42·5 parts of saliva are produced for the hundred of roast meat; 3·7 for as much of apples; and so on, according to the general rule above-stated. The quality of saliva is equally adapted to this end. It is easy to see how much more readily it mixes with most kinds of food than water alone does; and M. Bernard has shewn, that the saliva from the parotid, labial, and other small glands, being more aqueous than the rest, is that which is chiefly *braided* and mixed with

the food in mastication; while the more viscid mucoid secretion of the submaxiliary, palatine, and tonsillitic glands, is spread over the surface of the softened mass, to enable it to slide more easily through the fauces and œsophagus. This view obtains confirmation from the interesting fact pointed out by Professor Owen, that in the great ant-eater, whose enormously elongated tongue is kept moist by a large quantity of viscid saliva, the submaxillary glands are remarkably developed, while the parotids are not of unusual size (ccvii. p. 76, note).

Beyond these, its mechanical purposes, there are reasons for believing that saliva performs some chemical part in the digestion of the food. The chief of these reasons are, the number and size of the glands engaged in the secretion; the variety of substances which enter into its composition, and which can scarcely be supposed to be of use so far as its mechanical properties are concerned; the quantity which is secreted, not only during mastication, but after the food has passed into the stomach, especially in old persons, who from their loss of teeth, frequently swallow their food in an imperfectly masticated state; the fact that the saliva secreted during digestion is more alkaline than at other times; and lastly, the results of certain experiments.

Among the experiments are those of Spallanzani and Reaumur, who found that food inclosed in perforated tubes, and introduced into the stomach of an animal, was more quickly digested when it had been previously impregnated with saliva than when it was moistened with water. Dr. Wright also found that if the œsophagus of a dog is tied, and food mixed with water alone is placed in the stomach, the food will remain undigested though the stomach may secrete abundant acid fluid; but if the same food is mixed with saliva, and the rest of the experiment similarly performed, the food is readily digested.

But although it may hence appear that the saliva has more than a mechanical influence in promoting digestion, yet the

exact nature of the chemical part it takes is still somewhat uncertain. Its composition, as traced by chemical analysis, offers no certain guide. Its alkalinity, though as already stated, it appears to increase in the same proportion as the acidity of the secretion of the stomach both in health and disease, is never sufficient to neutralise the gastric fluid; the contents of the stomach, including as they do the saliva swallowed, are always acid. The very short time during which the saliva remains in contact with the food before it is neutralised by the acid of the stomach, precludes the notion that the alkali is the principal constituent by which it assists in digestion. Its organic principle, ptyaline, however, has evidently more power; for numerous experiments, easily repeated, shew that when saliva, or a portion of the salivary gland, or even a portion of dried ptyaline, is added to starch-paste, the starch is very rapidly transformed into dextrine and grape-sugar; and when common raw starch is masticated and mingled with saliva, and kept with it at a temperature of 90° or 100°, the starch-grains are cracked or eroded, and their contents are transformed in the same manner as the starch-paste. Changes similar to these are effected on the starch of farinaceous food (especially after cooking) in the stomach; and it is reasonable to refer them to the action of the saliva, because the acid of the gastric fluid tends to retard or prevent, rather than favour the transformation of the starch. It may therefore be held, that one purpose served by the saliva in the digestive process is that of assisting in the transformation of the starch, which enters so largely into the composition of most articles of vegetable food, and which (being naturally insoluble) is converted into soluble dextrine and grape-sugar, and made fit for absorption.

It appears from the experiments of Magendie (xviii. July, 1846) and Bernard (lix. 1847, p. 117), that, besides saliva, many azotised substances, especially if in a state of incipient decomposition, may excite this transformation of starch, such as pieces of the mucous membrane of the mouth, bladder,

rectum, and other parts, various animal and vegetable tissues, and even morbid products; but the gastric fluid will not produce the same effect. The property, therefore, cannot be exclusively assigned to the saliva, though, on the other hand, it seems proved by the experiments of Bidder and Schmidt (ccviii. pp. 17—18) that the transformation in question is effected much more rapidly by this fluid, than by any of the other fluids or substances experimented with, except the pancreatic secretion, which, as will be presently shewn, is very analogous to saliva. The actual process by which these changes are effected is still obscure. Probably the azotised substance, ptyaline, acts as a kind of ferment, like diastase in the process of malting, and excites molecular changes in the starch which result in its transformation, first into dextrine and then into sugar. According to Bernard, Magendie, Frerichs, and others, the part of the salivary fluid which is most active in thus transforming starch, is that secreted by the small glands of the mucous membrane of the mouth, the secretion of the true salivary glands having, according to Bernard, no influence on starch. Bidder and Schmidt however deny this, and believe that a mixture of the secretion of all the parts concerned in the formation of saliva is necessary to the perfect accomplishment of the metamorphosis (ccviii. p. 19).

The majority of observers agree that the transformation of starch into sugar ceases on the entrance of the food into the stomach, or on the addition of gastric fluid to it in a test-tube: while others maintain that it still goes on. Probably all are right: for although gastric fluid added to saliva appears to arrest the action of the latter on starch; yet, portions of saliva mingled with food in mastication may, for some time after their entrance into the stomach, remain unneutralised by the gastric secretion, and continue their influence upon the starchy principles in contact with them.

Starch appears to be the only principle of food upon which saliva acts chemically: it has no apparent influence on any of the other ternary principles, such as sugar, gum, mucus,

cellulose, or (according to Bernard) on fat: and seems to be equally destitute of power over albuminous and gelatinous substances, so that we have as yet no information respecting any purpose it can serve in the digestion of Carnivora, beyond that of softening or macerating the food; though, since such animals masticate their food very little, usually "bolting" it, the saliva has probably but little use even in this respect, in the process of digestion.*

### PASSAGE OF FOOD INTO THE STOMACH.

When properly masticated, the food is transmitted in successive portions to the stomach by the act of *deglutition* or *swallowing*. This act, for the purpose of description, may be divided into three parts. In the first, particles of food collected to a morsel glide between the surface of the tongue and the palatine arch, till they have passed the anterior arch of the fauces; in the second, the morsel is carried through the pharynx; and in the third, it reaches the stomach through the œsophagus. These three acts follow each other rapidly. The first is performed voluntarily by the muscles of the tongue and cheeks. The second also is effected with the aid of muscles which are in part endued with voluntary motion, such as the muscles of the soft palate and pharynx; but it is, nevertheless, an involuntary act, and takes place without our being able to prevent it, as soon as a morsel of food, drink, or saliva is carried backwards to a certain point of the tongue's surface. When we appear to swallow voluntarily, we only convey, through the first act of deglutition, a portion of food or saliva

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* For further information respecting the chemistry and action of saliva, reference may be made to Lehmann (cciii. vol. ii., and ccxxi.), Bidder and Schmidt (ccviii.), and a Review of their work by Dr. Day (cxc. vol. xii. p. 167), Valentin's and Scherer's reports to 1859 (lix.), Claude Bernard (ccxvii. 1856, and ccxiv. 1860), and Dr. Harley (cxc. Jan. 1860).

beyond the anterior arch of the palate; then the substance acts as a stimulus, which in accordance with the laws of reflex movements hereafter to be described, is carried by the sensitive nerves to the medulla oblongata, where it is reflected to the motor nerves, and an involuntary adapted action of the muscles of the palate and pharynx ensues. The third act of deglutition takes place in the œsophagus, the muscular fibres of which are entirely beyond the influence of the will.

The second act of deglutition is the most complicated, because the food must pass by the posterior orifice of the nose and the rima glottidis of the larynx, without touching them. When it has been brought, by the first act, behind the anterior arches of the palate, it is moved onwards by the tongue being carried backwards, and by the muscles of the anterior arches contracting behind it. The root of the tongue being retracted, and the larynx being raised with the pharynx and carried forwards under the tongue, the epiglottis is pressed over the rima glottidis, and the morsel glides past it; the closure of the glottis being additionally secured by the simultaneous contraction of its own muscles; so that, even when the epiglottis is destroyed, there is little danger of food or drink passing into the larynx, so long as its muscles can act freely. At the same time, the approximation of the sides of the posterior palatine arch, which move quickly inwards like side-curtains, closes the passage into the upper part of the pharynx and the posterior nares, and forms an inclined plane, along the under surface of which the morsel descends; then the pharynx, raised up to receive it, in its turn contracts, and forces it onwards into the œsophagus.

In the third act, in which the food passes through the œsophagus, every part of that tube, as it receives the morsel and is dilated by it, is stimulated to contract; hence an undulatory contraction of the œsophagus, which is easily observable in horses while drinking, proceeds rapidly along the tube. It is only when the morsels swallowed are large, or taken too quickly in succession, that the progressive contraction of the œsophagus

is slow, and attended with pain. Division of both pneumogastric nerves paralyses the contractile power of the œsophagus, and food accordingly accumulates in the tube (Bernard, ccxiv. July 7, 1860.)

Besides the actions ensuing in the œsophagus during the passage of food, certain rhythmic contractions have been observed at its lower part, independently of deglutition. They are produced by the fibres near the cardiac orifice of the stomach, which fibres are usually in a state of contraction, especially when the stomach is full, and appear to act as a kind of sphincter to prevent the regurgitation of food. During vomiting they are relaxed; and at the same time, the whole muscular tissue of the tube is said to perform an anti-peristaltic motion, the reverse of that which it executes during deglutition. When vomiting has been produced by the injection of tartar emetic into the veins, these anti-peristaltic motions of the œsophagus are said to be continued, even though the tube is separated from the stomach.

## DIGESTION OF FOOD IN THE STOMACH.

### *Structure of the Stomach.*

It appears to be an almost universal character of animals, that they have an internal cavity for the production of a chemical change in the aliment—a cavity for digestion: and when this cavity is compound, the part in which the food undergoes its principal and most important changes is the stomach.

In man, and those Mammalia which are provided with a single stomach, its walls consist of three distinct layers or coats, viz., an external peritoneal, an internal mucous, and an intermediate muscular coat, with blood-vessels, lymphatics, and nerves distributed in and between them. In relation to the physiology of the stomach in digestion, only the muscular and mucous coats need be considered.

The *muscular coat* of the stomach consists of three separate

layers or sets of fibres, which, according to their several directions, are named the longitudinal, circular, and oblique. The *longitudinal* set are the most superficial: they are continuous with the longitudinal fibres of the œsophagus, and spread out in a diverging manner over the great end and sides of the stomach. They extend as far as the pylorus, being especially distinct at the lesser or upper curvature of the stomach, along which they pass in several strong bands. The next set are the *circular* or *transverse* fibres, which more or less completely encircle all parts of the stomach; they are most abundant at the middle and in the pyloric portion of the organ, and some form the chief part of the thick projecting ring of the pylorus. The next, and consequently deepest set of fibres, are the *oblique;* they are comparatively few in number, and are placed only at the cardiac orifice and portion of the stomach, over both surfaces of which they are spread, some passing obliquely from left to right, others from right to left, around the cardiac orifice, to which, by their interlacing, they form a kind of sphincter, continuous with that round the lower end of the œsophagus. The fibres of which the several muscular layers of the stomach, and of the intestinal canal generally, are composed, belong to the class of organic muscle, being smooth or unstriped, elongated, spindle-shaped fibre-cells, a fuller description of which will be given under the head of Muscular tissue.

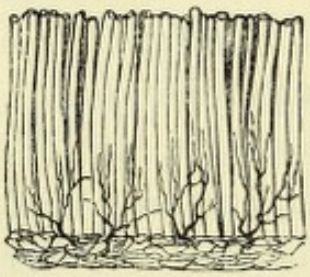
The *mucous membrane* of the stomach rests upon a layer of loose cellular membrane, or submucous tissue, which connects it with the muscular coat, and contains its principal blood-vessels. Examined when the stomach is distended, it is smooth, level, soft, and velvety; in the contracted state, it is thrown into numerous, chiefly longitudinal, folds or rugæ. When examined with a lens, the internal or free surface, as was first accurately pointed out by Dr. Sprott Boyd (xciv. vol. xlvi.), presents a peculiar honeycomb appearance, produced by shallow, polygonal depressions or cells (fig. 19, A.) the diameter of which varies gene-

rally from $\frac{1}{200}$th to $\frac{1}{350}$th of an inch; but near the pylorus is as much as $\frac{1}{100}$th of an inch. They are separated by slightly elevated ridges which sometimes, especially in certain morbid states of the stomach, bear minute, narrow, vascular processes that look like villi, and have given rise to the erroneous supposition, that the stomach has absorbing villi like those of the small intestines. In the bottom of the cells minute openings are visible (fig. 19, A), which are the orifices of perpendicularly-arranged tubular glands imbedded side by side in sets or bundles, in the substance of the mucous membrane, and composing (B) nearly the whole structure.

*Fig.* 19.*

A

B



These tubular glands (fig. 20, *a* and fig. 21) vary in length from one-fourth of a line to nearly a line; they are longer and more thickly set towards the pylorus than elsewhere; their length is equal to the various thickness of the mucous membrane of the stomach at different parts. At their bases, which rest on the submucous tissue, or an intervening layer of muscular tissue (fig. 20, *b*) they measure about $\frac{1}{300}$th of an inch in diameter, and at their orifices about $\frac{1}{500}$th. Sometimes their blind dilated extremities, instead of being rounded off have an uneven, or varicose, or pouched appearance, and sometimes they are slightly branched. Occasionally two contiguous tubules coalesce above, and open on the surface of the stomach by a common orifice or duct. Their walls consist essentially of tubular inflections of the basement membrane of the

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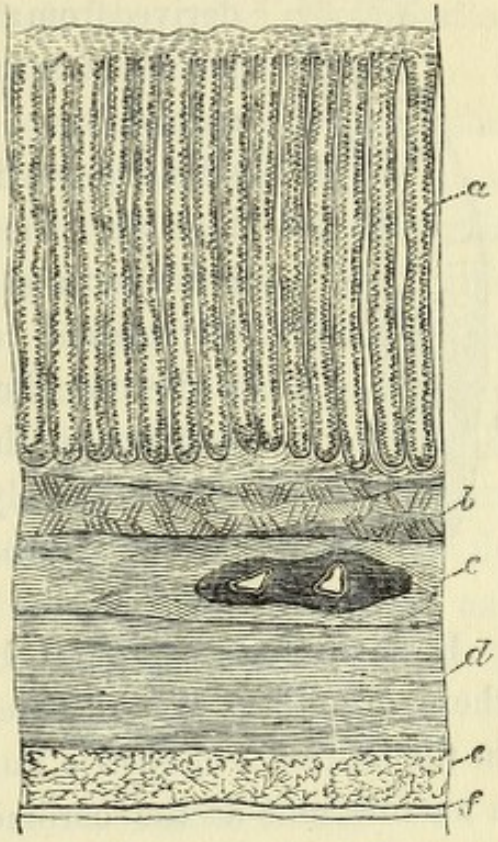
* Fig. 19. Mucous membrane of the stomach, after Boyd. A Cells of human stomach,—open mouths of tubes seen at the bottom of each,—magnified 32 diameters; B. Section of mucous membrane of the stomach in the pig,—the cellular coat on which the bases of the tubes rest has been injected,—magnified about 20 diameters.

mucous coat of the stomach. This membrane, in the upper third of the tube, is lined by an epithelial layer of cylindrical cells, continuous with that of the surface of the stomach: in the lower two-thirds, instead of a layer of cylindrical epithelium, the tube is filled by numerous roundish, or oval, or polygonal nucleated cells, in various stages of development, containing much finely granular material, and engaged in the secretion of the gastric fluid, which, when fully elaborated, is discharged by the cells, and mixes with the food in the stomach. These cells have been named by Frerichs peptic cells, because of the pepsine of the gastric fluid being contained within them. The tubes or glands in which they occur, are also named *peptic* glands (Kölliker.)

*Fig.* 20.*

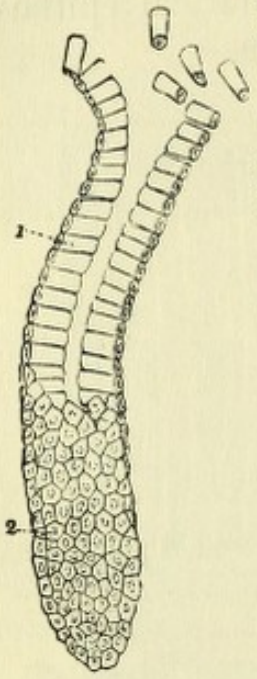



The cylindrical cells in the upper part of the tube appear to take no direct share in the secretion of the acid gastric juice; but assist in forming the neutral or slightly alkaline mucus which covers the surface of the stomach during fasting (Kölliker, ccvi. p. 399). In the intervals between successive periods of digestion, when the stomach is empty, the lower secreting parts of the tubules appear to be at rest, and are said to be nearly empty: they are called into activity on the fresh introduction of food. The elaboration of the gastric or digestive fluid in the cells seems to be perfected only as they reach the surface; for, accord-

* Fig. 20.—Longitudinal section through the coats of a pig's stomach, near the pylorus; magnified 30 diameters.—*a*. Tubular glands of the mucous membrane. *b*. A layer of muscular tissue. *c*. Submucous tissue, containing nerves and blood-vessels, two of the latter cut across. *d*. Transverse muscular coat. *e*. Longitudinal muscular coat. *f*. Serous layer. (After Kölliker).

ing to Bernard (xix. March, 1844), the mucous membrane is not acid a little below the surface.

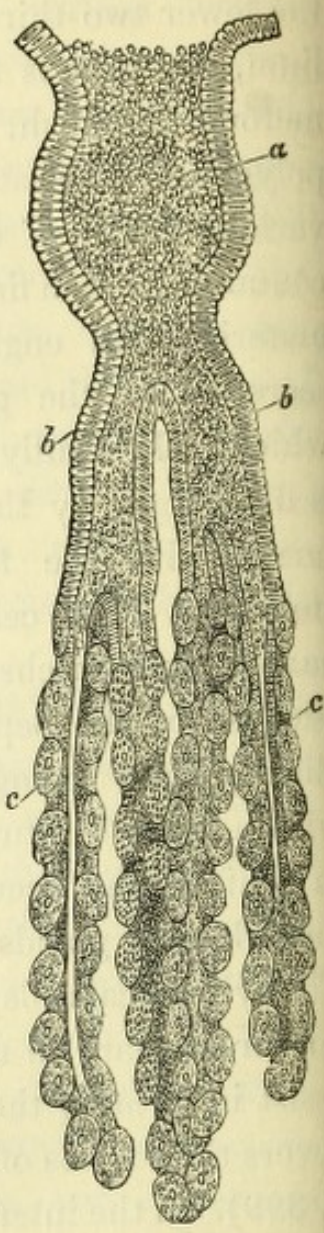
*Fig.* 21.*




On their outside, these tubular glands are covered by capillary blood-vessels derived from arteries, whose principal trunks lie in the submucous tissue, and send up vertical branches through the interspaces between the several bundles of glands (fig. 19, B); while branches form anastomoses in the ridges between the polygonal spaces on the internal surface of the stomach.

Besides these simple tubular glands, there are others also, apparently engaged in the secretion of gastric fluid, occupying a narrow zone at the cardiac end of the stomach, and differing in being compound, or branched into three, five, or seven tubes, filled with large peptic cells, and presenting a peculiar varicose or beaded appearance (fig. 22.) These compound

*Fig.* 22.†

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* Fig. 21. — One of the tubular follicles of a pig's stomach, after Wasmann, cut obliquely so as to display the upper part of its cavity, with the cylindrical epithelium forming its walls. At the lower part of the follicle, the external nucleated extremities of the cylinders of epithelium are seen.

† Fig. 22.—Gastric gland from the stomach of a dog. *a*. Upper part of the tube lined by cylindrical epithelium. *b*. Primary branches, with similar epithelium. *c*. Terminal branches filled with secreting gland-cells, and exhibiting a central canal for the escape of the secreted fluid. (After Kölliker.)

glands are well-marked in some animals, especially the dog.

Near the pylorus, there appear, also, to be a number of compound tubular glands, which differ from the last in containing no peptic cells, but in being lined throughout with cylindrical epithelium and apparently engaged in the formation of simple mucus. Kölliker names them mucous glands.

Besides the proper gastric and mucous glands, certain other glandular structures are frequently met with in the stomach both of man and animals. These are small opaque-white sacculi, like Peyer's solitary glands of the intestines, filled with minute cells and granules, situated chiefly along the lesser curvature of the stomach beneath the mucous membrane, sometimes in the pyloric regions also. They are said to be only found during digestion in man; and it is probable that, having elaborated certain materials of importance to the digestive process, they burst, discharge their contents, and disappear. According to Brinton, they are rarely absent in children.*

### *Secretion and Properties of the Gastric Fluid.*

While the stomach contains no food, and is inactive, no gastric fluid is secreted; and mucus, which is either neutral or slightly alkaline, covers its surface. But immediately on the introduction of food or other foreign substance into the stomach, the mucous membrane, previously quite pale, becomes slightly turgid and reddened with the influx of a larger quantity of blood; the gastric glands commence secreting actively, and an acid fluid is poured out in minute drops, which gradually run together and flow down the walls of the stomach, or soak into the substances introduced.

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* For the best recent account of the structure of the mucous membrane of the stomach, see Kölliker (ccvi. p. 398; ccxii; and ccxviii, p. 319, 1860), and Brinton (lxxiii. Art. "Stomach and Intestines"), who confirms Kölliker's description, and adds much original matter.

The nature of the *gastric fluid* thus secreted, was till lately involved in complete obscurity. The first accurate analysis of it was made by Dr. Prout; but it does not appear that it was collected in any large quantity, or pure and separate from food, until the time when Dr. Beaumont (cxxxviii,) was enabled by a fortunate circumstance, to obtain it from the stomach of a man, named St. Martin, in whom there existed, as the result of a gunshot wound, an opening leading directly into the stomach, near the upper extremity of the great curvature, and three inches from the cardiac orifice. The external opening was situated two inches below the left mamma, in a line drawn from that part to the spine of the left ilium. The borders of the opening into the stomach, which was of considerable size, had united, in healing, with the margins of the external wound; but the cavity of the stomach was at last separated from the exterior by a fold of mucous membrane, which projected from the upper and back part of the opening, and closed it like a valve, but could be pushed back with the finger. The introduction of any mechanical irritant, such as the bulb of a thermometer, into the stomach, excited at once the secretion of gastric fluid. This could be drawn off with a caoutchouc tube, and could often be obtained to the extent of nearly an ounce. The introduction of alimentary substances caused a much more rapid and abundant secretion of pure gastric fluid than the presence of other mechanical irritants did. No increase of temperature could be detected during the most active secretion; the thermometer introduced into the stomach, always stood at 100° Fah., except during muscular exertion, when the temperature of the stomach, like that of other parts of the body, rose one or two degrees higher.

M. Blondlot (xvi.) and subsequently M. Bernard (xix. June, 1844), and since then, several others, by maintaining fistulous openings into the stomachs of dogs, have confirmed most of the facts discovered by Dr. Beaumont. From their observations, also, it appears, that pepper, salt, and other soluble stimulants excite a more rapid discharge of gastric fluid than mechanical

irritation does; so do alkalies generally, but acids have a contrary effect. When mechanical irritation is carried beyond certain limits so as to produce pain, the secretion, instead of being more abundant, diminishes or ceases entirely, and a ropy mucus is poured out instead. Very cold water, or small pieces of ice, at first render the mucous membrane pallid, but soon a kind of reaction ensues, the membrane becomes turgid with blood, and a larger quantity of gastric juice is poured out. The application of too much ice is attended by diminution in the quantity of fluid secreted, and by consequent retardation of the process of digestion. The quantity of the secretion seems to be influenced also by impressions made on the mouth; for Blondlot found that when sugar was introduced into the dog's stomach, either alone, or mixed with human saliva, a very small secretion ensued; but when the dog had himself masticated and swallowed it, the secretion was abundant.

Dr. Beaumont described the secretion of the human stomach as "a clear transparent fluid, inodorous, a little saltish, and very perceptibly acid. Its taste is similar to that of thin mucilaginous water, slightly acidulated with muriatic acid. It is readily diffusible in water, wine, or spirits; slightly effervesces with alkalies; and is an effectual solvent of the *materia alimentaria*. It possesses the property of coagulating albumen in an eminent degree; is powerfully antiseptic, checking the putrefaction of meat; and effectually restorative of healthy action, when applied to old fœtid sores and foul ulcerating surfaces" (p. 76).

Dr. Dunglison found in this gastric fluid free hydrochloric and acetic acids, phosphates and hydrochlorates of potash, soda, lime, and magnesia, and an animal matter which was soluble in cold, but insoluble in hot water. The quantity of free hydrochloric acid which he obtained by distillation, seems to have been large; and Dr. Prout, as well as other chemists, have satisfied themselves of the existence of this acid in the gastric fluid of the rabbit, hare, horse, calf, and dog. Acetic acid

also, is said to have been found in the gastric secretion of horses and dogs, as well as by Dr. Beaumont in that of the human subject. But the results of more recent experiments by M. Blondlot (xvi. and later still, lix. 1859), Dr. R. D. Thompson (xvii. May, 1845), MM. Bernard and Barreswil (xviii. Dec. 1844), and Lehmann (lix. 1847, p. 102), cast doubt on the opinion that *free* hydrochloric, acetic, or any other volatile acid, exists in this fluid; at least in the case of the dog and pig, the animals experimented on. Having obtained large quantities of pure gastric fluid from the stomach of a dog, and carefully distilled portions of it on the sand-bath, Blondlot found not the slightest trace of acidity in the product of the distillation; but the residue of the retort was intensely acid, and became more so the more it was concentrated by continuing the distillation. The non-existence of both hydrochloric and acetic acids seeming to be thus demonstrated, Blondlot was led to believe that the acidity of the gastric fluid depends on an acid phosphate of lime. For he observed no effervescence on the addition of carbonate of lime to the acid gastric fluid; neither when carbonate of lime was placed in the gastric fluid, was the fluid neutralized, or the carbonate dissolved. By further investigation, he demonstrated the existence of a super-phosphate of lime in the gastric fluid. But he seems to have been in error in attributing the whole of the acidity of the gastric fluid to this salt: for MM. Bernard and Barreswil have found that if the gastric fluid be sufficiently concentrated by evaporation, distinct effervescence occurs on the addition of carbonate of lime; proving the presence of some free acid, which they, as well as Dr. R. D. Thompson, Lehmann (lix. 1847, p. 102), and Frerichs (lix. 1850, p. 134), consider to be the lactic, an opinion to which Liebig (liv. p. 138) also gives his sanction. MM. Melsens and Dumas (lix. 1844, p. 109), have also proved the existence of a free acid by the gradual solution of portions of carbonate of lime placed in gastric fluid. But since, even after long contact, the carbonate of lime does not completely neutralize the acid of the gastric fluid, it is most probable that

there is, together with a free acid, some acid phosphate of lime, as maintained by M. Blondlot.

Respecting the nature of the free acid, whose presence is thus proved, the discrepant results suggest a supposition that the source of the acidity of the gastric fluid may vary in different animals, or at different times in the same animal. The existence of hydrochloric acid in the human gastric fluid seems to have been clearly determined by Prout, Dunglison, Enderlin (lix. 1843, p. 149), and others (see especially, Hübbenet, cxciv.), and more recently by Professor Graham (ccvii. p. 82); its non-existence, and the existence of lactic acid, as clearly in the fluid of pigs and dogs by the other analysts just quoted, and more recently by Bernard (ccxvii. p. 393); possibly all are right. The results of experiments in artificial digestion make it probable, that the digestive properties of the gastric fluid require only the existence of a certain degree of acidity, which is equally effective whatever be the acid employed, provided this acid does not decompose the active animal principle of the digestive fluid.*

The *animal matter* mentioned in the analysis of the gastric fluid by Dr. Dunglison has been since named *pepsine*, from its power in the process of digestion. It is an azotised substance, the composition of which, according to Bidder and Schmidt (ccviii. p. 46), consists of $C_{53}H_{6\cdot7}N_{17\cdot8}$ and $O_{22\cdot5}$. It is best procured by digesting portions of the mucous membrane of the stomach in cold water, after they have been macerated for some time in water at a temperature between 80° and 100° F. The warm water dissolves various substances as well as some of the pepsine, but the cold water takes up little else than pepsine, which, on evaporating the cold solution, is obtained in a greyish-brown viscid fluid. The addition of

* An excellent summary of our knowledge on this subject is given by Dr. Brinton in his elaborate article on the Stomach and Intestines, in Todd's Cyclopædia of Anatomy and Physiology, June, 1855.

alcohol throws down the pepsine in greyish-white flocculi; and one part of the principle thus prepared, if dissolved in even 60,000 parts of water, will digest meat and other alimentary substances.

The *digestive power of the gastric fluid* is manifested in its softening, reducing into pulp, and partially or completely dissolving various articles of food placed in it at a temperature of from 90° to 100°. This, its peculiar property, requires the presence of both the pepsine and the acid; neither of them can digest alone, and when they are mixed, either the decomposition of the pepsine, or the neutralization of the acid, at once destroys the digestive property of the fluid. For the perfection of the process also certain conditions are required, which are all found in the stomach; namely, first, a temperature of about 100° F.; secondly, such movements as the food is subjected to by the muscular actions of the stomach, which bring in succession every part of it in contact with the mucous membrane, whence the fresh gastric fluid is being secreted; thirdly, the constant removal of those portions of food which are already digested, so that what remains undigested may be brought more completely into contact with the solvent fluid; and fourthly, a state of softness and minute division, such as that to which the food is reduced by mastication previous to its introduction into the stomach.

The chief circumstances connected with the mode in which the gastric fluid acts upon food during natural digestion, have been determined by watching its operations on different alimentary substances, when removed from the stomach and placed in conditions as nearly as possible like those under which it acts while within that viscus. The fact that solid food, immersed in gastric fluid out of the body, and kept at a temperature of about 100°, is gradually converted into a thick fluid similar to chyme, was shewn by Spallanzani, Dr. Stevens, Tiedemann and Gmelin, and others. They used the gastric fluid of dogs,—obtained by causing the animals to swallow

small pieces of sponge, which were subsequently withdrawn, soaked with the fluid,—and proved nearly as much as the later experiments with the same kind of gastric fluid by Blondlot, Bernard, and others. But these need not be particularly referred to, while we have the more satisfactory and instructive observations which Dr. Beaumont made with the fluid obtained from the stomach of St. Martin. After the man had fasted seventeen hours, Dr. Beaumont took one ounce of gastric fluid, put into it a solid piece of boiled recently salted beef weighing three drachms, and placed the vessel which contained them in a water-bath heated to 100°. "In forty minutes, digestion had distinctly commenced over the surface of the meat; in fifty minutes, the fluid had become quite opaque and cloudy, the external texture began to separate and become loose; and in sixty minutes chyme began to form. At 1 p.m." (two hours after the commencement of the experiment) "the cellular texture seemed to be entirely destroyed, leaving the muscular fibres loose and unconnected, floating about in small fine shreds, very tender and soft" (cxxxviii. p. 120). In six hours, they were nearly all digested — a few fibres only remaining. After the lapse of ten hours, every part of the meat was completely digested. The gastric juice which was at first transparent, was now about the colour of whey, and deposited a fine sediment of the colour of meat. A similar piece of beef was, at the time of the commencement of this experiment, suspended in the stomach by means of a thread; at the expiration of the first hour it was changed in about the same degree as the meat digested artificially; but, at the end of the second hour, it was completely digested and gone.

In other experiments, Dr. Beaumont withdrew, through the opening of the stomach, some of the food which had been taken twenty minutes previously, and which was completely mixed with the gastric juice. He continued the digestion, which had already commenced, by means of artificial heat in a water-bath. In a few hours, the food thus treated was

completely chymified; and the artificial seemed in this, as in several other experiments, to be exactly similar to, though a little slower than, the natural digestion.

The apparent identity of the process within and out of the stomach thus manifested, while it shews that we may regard digestion as essentially a chemical process, when once the gastric fluid is formed, justifies the belief that Dr. Beaumont's other experiments with the digestive fluid may exactly represent the modifications to which, under similar conditions, its action in the stomach would be liable. He found that, if the mixture of food and gastric fluid were exposed to a temperature of 34° F., the process of digestion was completely arrested. In another experiment, a piece of meat which had been macerated in water at the temperature of 100° for several days, till it acquired a strong putrid odour, lost, on the addition of some fresh gastric juice, all signs of putrefaction, and soon began to be digested. From other experiments he obtained the data for estimates of the degrees of digestibility of various articles of food, and the modes in which the digestion is liable to be affected, to which reference will again be made.

When natural gastric juice cannot be obtained, many of these experiments may be performed with an *artificial digestive fluid*, the action of which, probably, very closely resembles that of the fluid secreted by the stomach. It is made by macerating in water portions of fresh dried mucous membrane of the stomach of a pig* or other omnivorous animal, or of the fourth stomach of the calf, and adding to the infusion a few drops of hydrochloric acid—about 3·3 grains to half an ounce of the mixture, according to Schwann. Portions of food placed in such fluid, and maintained with it at a temperature of about

* The best portion of the stomach of the pig for this purpose is that between the cardiac and pyloric orifices; the cardiac portion appears to furnish the least active digestive fluid.

100°, are, in an hour or more, according to the toughness of the substance, softened and changed in just the same manner as they would be in the stomach.

The nature of the action by which the mucous membrane of the stomach and its secretion, work these changes in organic matter, is exceedingly obscure. The action of the pepsine may be compared with that of a ferment, which at the same time that it undergoes change itself, induces certain changes also in the organic matters with which it is in contact. Or its mode of action may belong to that class of chemical processes termed "catalytic," in which a substance excites, by its mere presence, and without itself undergoing change as ordinary ferments do, some chemical action in the substances with which it is in contact. So, for example, spongy platinum, or charcoal, placed in a mixture, however voluminous, of oxygen and hydrogen, makes them combine to form water; and diastase makes the starch in grains undergo transformation, and sugar is produced. And that pepsine acts in some such manner appears probable from the very minute quantity capable of exerting the peculiar digestive action on a large quantity of food, and apparently with little diminution in its active power. The process differs from ordinary fermentation in being unattended with the formation of carbonic acid, in not requiring the presence of oxygen, and in being unaccompanied by the production of new quantities of the active principle, or ferment. It agrees with the processes of both fermentation and organic catalysis, in that whatever alters the composition of the pepsine (such as heat above 100°, strong alcohol, or strong acids), destroys the digestive power of the fluid.

### *Changes of the Food in the Stomach.*

The general effect of digestion in the stomach is the conversion of the food into *chyme*, a substance of various composition according to the nature of the food, yet always presenting a

characteristic thick, pultaceous, grumous consistence, with the undigested portions of the food mixed in a more fluid substance, and a strong disagreeable acid odour and taste. Its colour depends on the nature of the food, or on mixtures of yellow or green bile which may, apparently even in health, pass into the stomach.

Reduced into such a substance, all the various materials of a meal may be mingled together, and near the end of the digestive process hardly admit of recognition; but the experiments of artificial digestion, and the examination of stomachs with fistulæ, have illustrated many of the changes through which the chief alimentary principles pass, and the times and modes in which they are severally disposed of. These must now be traced.

The readiness with which the gastric fluid acts on the several articles of food is, in some measure, determined by the state of division, and the tenderness and moisture of the substance presented to it. By minute division of the food, the extent of surface with which the digestive fluid can come in contact is increased, and its action proportionably accelerated. Tender and moist substances offer less resistance to the action of the gastric juice than tough, hard, and dry ones do, because they may be thoroughly penetrated with it, and thus be attacked by it, not only at the surface, but at every part at once. The readiness which which a substance is acted upon by the gastric fluid does not, however, necessarily imply the degree of its nutritive property; for a substance may be nutritious, yet, on account of its toughness and other qualities, hard to digest; and many soft, easily-digested substances contain comparatively a small amount of nutriment. But for a substance to be nutritive, it must be capable of being assimilated to the blood; and to find its way into the blood, it must, if insoluble, be digestible by the gastric fluid or some other secretion in the intestinal canal. There is, therefore, thus far, a necessary connection between the digestibility of a substance and its power of affording nutriment.

Those portions of food which are liquid when taken into the stomach, or which are easily soluble in the fluids therein, are probably at once absorbed by the blood-vessels in the mucous membrane of the stomach. Magendie's experiments, and better still, those of Dr. Beaumont, have proved this quick absorption of water, wine, weak saline solutions, and the like; that they are absorbed without manifest change by the digestive fluid; and that, generally, the water of such liquid food as soups is absorbed at once, so that the substances suspended in it are concentrated into a thicker material, like the chyme from solid food, before the digestive fluid acts upon them.

The *action of the gastric fluid* on the several kinds of *solid food* has been studied in various ways. In the earliest experiments, perforated metallic and glass tubes, filled with the alimentary substances, were introduced into the stomachs of animals, and after the lapse of a certain time withdrawn, to observe the condition of the contained substances; but such experiments are fallacious, because gastric fluid has not ready access to the food. A better method was practised in a series of experiments by Tiedemann and Gmelin, who fed dogs with different substances, and killed them in a certain number of hours afterwards. But the results they obtained are of less interest than those of the experiments of Dr. Beaumont, on his patient, St. Martin, and of Dr. Gosse (cxxxvii.) who had the power of vomiting at will.

Dr. Beaumont's observations shew, that the process of digestion in the stomach, during health, takes place so rapidly, that a full meal, consisting of animal and vegetable substances, may nearly all be converted into chyme in about an hour, and the stomach left empty in two hours and a half. The details of two days' experiments will be sufficient examples:—

Exp. 42. April 7th, 8 A.M. St. Martin breakfasted on three hard-boiled eggs, pancakes, and coffee. At half-past eight o'clock, Dr. Beaumont examined the stomach, and found a heterogeneous mixture of the several articles slightly

digested . . . . At a quarter past ten, no part of the breakfast remained in the stomach.

Exp. 43.—At eleven o'clock the same day, he ate two roasted eggs and three ripe apples. In half an hour they were in an incipient state of digestion; and a quarter past twelve no vestige of them remained.

Exp. 44.—At two o'clock P.M. same day, he dined on roasted pig and vegetables. At three o'clock they were half chymified, and at half-past four nothing remained but a very little gastric juice.

Again, Exp. 46. April 9th. At three o'clock P.M. he dined on boiled dried codfish, potatoes, parsnips, bread, and drawn butter. At half-past three o'clock examined, and took out a portion about half digested; the potatoes the least so. The fish was broken down into small filaments; the bread and parsnips were not to be distinguished. At four o'clock, examined another portion. Very few particles of fish remained entire. Some of the few potatoes were distinctly to be seen. At half-past four o'clock, took out and examined another portion; all completely chymified. At five o'clock, stomach empty (p. 158).

Many circumstances besides the nature of the food are apt to influence the process of chymification. Among them are, the quantity of food taken; the stomach should be fairly filled, not distended: the time that has elapsed since the last meal, which should be at least enough for the stomach to be quite clear of food: the amount of exercise previous and subsequent to the meal, gentle exercise being favourable, over-exertion injurious to digestion; the state of mind, tranquillity of temper being apparently essential to a quick and due digestion: the bodily health: the state of the weather. But under ordinary circumstances, from three to four hours may be taken as the average time occupied by the complete digestion of a meal.

Dr. Beaumont constructed a table shewing the times required for the digestion of all usual articles of food in St. Martin's stomach, and in his gastric fluid taken from the stomach. Among the substances most quickly digested were rice and

tripe, both of which were chymified in an hour; eggs, salmon, trout, apples, and venison, were digested in an hour and a half; tapioca, barley, milk, liver, fish, in two hours; turkey, lamb, potatoes, pig, in two hours and a half; beef and mutton required from three hours to three and a half, and both were more digestible than veal; fowls were like mutton in their degree of digestibility. Animal substances were, in general, converted into chyme more rapidly than vegetables.

Dr. Beaumont's experiments were all made on ordinary articles of food. A minuter examination of the changes produced by gastric digestion on various tissues has been made by Dr. Rawitz (xxvi.), who examined microscopically the products of the artificial digestion of different kinds of food, and the contents of the fæces after eating the same kinds of food. The general results of his examinations, as regards *animal* food, shew that muscular tissue breaks up into its constituent fasciculi, and that these again are divided transversely; gradually the transverse striæ become indistinct, and then disappear; and finally, the sarcolemma seems to be dissolved, and no trace of the tissue can be found in the chyme, except a few fragments of fibres. These changes ensue most rapidly in the flesh of fish and hares, less rapidly in that of poultry and other animals. The fragments of muscular tissue which remain after the continued action of the digestive fluid, do not, according to Rawitz, undergo any alteration in their passage through the rest of the intestinal canal; for he found similar fragments in fæces even twenty-four hours after the introduction of the meat into the stomach. Bidder and Schmidt, however, have shewn clearly that muscular fibres may be completely digested in the intestines. The cells of cartilage and fibro-cartilage, except those of fish, pass unchanged through the stomach and intestines, and may be found in the fæces. The interstitial tissues of these structures are converted into pulpy textureless substances in the artificial digestive fluid, and are not discoverable in the fæces. Elastic fibres are unchanged in the digestive fluid. Fatty matters also are unchanged; fat-cells

are sometimes found quite unaltered in the fæces: and crystals of cholestearine may usually be obtained from fæces, especially after the use of pork-fat.

As regards *vegetable* substances, Dr. Rawitz states, that he frequently found large quantities of cell-membranes unchanged in the fæces; also starch-cells, commonly deprived of only part of their contents. The green colouring principle, chlorophyll, was usually unchanged. The walls of the sap-vessels and spiral-vessels were quite unaltered by the digestive fluid, and were usually found in large quantities in the fæces; their contents, probably, were removed.

From these experiments, we may understand the *structural* changes which the chief alimentary substances undergo in their conversion into chyme; and the proportions of each which are not reducible to chyme, nor capable of any further act of digestion. The *chemical* changes undergone in and by the proximate principles are less easily traced.

Of the *albuminous* principles, the caseine of milk, and, according to Dr. Beaumont, fluid albumen, are coagulated by the acid of the gastric fluid; and thus, before they are digested, come into the condition of the other solid principles of the food. These, including solid albumen and fibrine, in the same proportion as they are broken up and anatomically disorganised by the gastric fluid, appeared to be reduced or *lowered* in their chemical composition (see Prout, xxi. p. 463). This chemical change is probably produced, as suggested by Dr. Prout, by the principles entering into combination with water. It is sufficient to conceal nearly all their characteristic properties; the albumen is rendered scarcely coagulable by heat; the gelatine, even when its solution is evaporated, does not congeal in cooling; the fibrine and caseine cannot be found by their characteristic tests. It would seem, indeed, that all these various substances are converted into one and the same principle, a low form of albumen, not precipitable by nitric acid or heat, and now generally termed *albuminose* or *peptone*, from which, after being absorbed, they are again

raised in the elaboration of the chyle and blood to which they are assimilated.

Whatever be the mode in which the gastric secretion affects these principles, it, or something like it, appears essential, in order that they may be assimilated to the blood and tissues. For, when Bernard and Barreswil injected albumen dissolved in water into the jugular veins of dogs, they always, in about three hours after, found it in the urine. But if, previous to injection, it was mixed with gastric fluid, no trace of it could be detected in the urine. The influence of the liver seems to be almost as efficacious as that of the gastric fluid, in rendering albumen assimilable; for Bernard found that, if diluted egg-albumen, unmixed with gastric fluid, is injected into the portal vein, it no longer makes its appearance in the urine, and is, therefore, no doubt, assimilated by the blood (xix, 1850, p. 889).

The *saccharine* including the *amylaceous* principles are at first, probably, only mechanically separated from the vegetable substances within which they are contained, by the action of the gastric fluid. The soluble portions, viz., dextrine, sugar, and gum, are probably at once absorbed. The insoluble ones, viz., starch and lignine (or some parts of it) are rendered soluble and capable of absorption, by being converted into dextrine or grape-sugar. It is probable that this change is carried on to some extent in the stomach; the recent experiments of Bardeleben and Brown-Séquard may be especially referred to, in confirmation of this view (lix. 1859, p. 37; and ccxviii. 1858). This conversion of starch into sugar is probably effected, however, not by the gastric fluid, but by the saliva introduced with the food, or subsequently swallowed; for Frerichs found that it was arrested if, by tying the œsophagus, the continued introduction of salivary secretion into the stomach was prevented (xv. Bd. 3, Art. Verdauung); and, even in those cases in which it is said to go on, when the access of saliva is prevented, it may, as Valentin suggests (lix. 1859, p. 37), be perhaps ascribed to some of the secretion of

Brunner's glands, or of the pancreas, having entered the stomach. The transformation of starch is continued in the intestinal canal, probably, as will be shewn, by the secretion of the pancreas, and by that of the intestinal glands and mucous membrane. The power of digesting uncooked starch is probably very limited in man and Carnivora, for when starch has been taken raw, as in corn and rice, large quantities of the granules are passed unaltered with the excrements. Cooking, by expanding or bursting the envelopes of the granules, renders their interior more amenable to the action of the digestive organs; and the abundant nutriment furnished by bread, and the large proportion that is absorbed of the weight of it consumed, afford proof of the completeness of their power to make its starch soluble and prepare it for absorption. According to Blondlot, component particles of starch-grains are held together by an azotised substance analogous to gelatine; he believes, that the gastric fluid dissolves this substance, and that the liberated minute particles of starch are not further chemically acted upon in the alimentary canal, but, with the fatty, albuminous, and other molecules of chyle, are taken up by the intestinal villi (lix. 1856, p. 172).

Of the *oleaginous principles*, as to their changes in the stomach, no more can be said, than that they appear to be reduced to minute particles, and pass into the intestines mingled with the other constituents of the chyme. Being further changed in the intestinal canal, they are rendered capable of absorption by the lacteals.

### *Movements of the Stomach.*

It has been already said, that the gastric fluid is assisted towards accomplishing its share in digestion by the movements of the stomach. In granivorous birds, for example, the contraction of the strong muscular gizzard affords a necessary aid to digestion by grinding and triturating the hard seeds which constitute part of the food. But in the stomachs of man and Mammalia the motions of the muscular coat are too feeble to

exercise any such mechanical force on the food; neither are they needed, for mastication has already done the mechanical work of a gizzard; and the experiments of Reaumur and Spallanzani have demonstrated that substances enclosed in perforated tubes, and consequently protected from mechanical influence, are yet digested.

The normal actions of the muscular fibres of the human stomach appear to have a three-fold purpose; first, to adapt the stomach to the quantity of food in it, so that its walls may be in contact with the food on all sides, and, at the same time, may exercise a certain amount of compression upon it; secondly, to keep the orifices of the stomach closed until the food is digested; and, thirdly, to perform certain peristaltic movements, whereby the food, as it becomes chymified, is gradually propelled towards, and ultimately through, the pylorus. In accomplishing this latter end, the movements will, no doubt, materially contribute towards effecting a thorough intermingling of the food and the gastric fluid.

When digestion is not going on, the stomach is uniformly contracted, its orifices not more firmly than the rest of its walls; but, if examined shortly after the introduction of food, it is found closely encircling its contents, and its orifices are firmly closed like sphincters. The cardiac orifice, every time food is swallowed, opens to admit its passage to the stomach, and immediately again closes. The pyloric orifice, during the first part of gastric digestion, is usually so completely closed, that even when the stomach is separated from the intestines, none of its contents escape. But towards the termination of the digestive process, the pylorus seems to offer less resistance to the passage of substances from the stomach; first it yields to allow the successively digested portions to go through it; and then it allows the transit of even undigested substances.

From the observations of Dr. Beaumont on the man St. Martin, it appears that food, so soon as it enters the stomach, is subjected to the action of the muscular coat, whereby

the digested portions are gradually approximated towards the pylorus. The movements were observed to increase in rapidity as the process of chymification advanced, and were continued until it was completed.

The contraction of the fibres situated towards the pyloric end of the stomach, seems to be more energetic and more decidedly peristaltic than those of the cardiac portion. Thus, Dr. Beaumont found that when the bulb of the thermometer was placed about three inches from the pylorus, it was tightly embraced from time to time and drawn towards the pyloric orifice for a distance of three or four inches. The object of this movement appears to be, as just said, to carry the food towards the pylorus as fast as it is formed into chyme, and to propel the chyme into the duodenum; the undigested portions of food being kept back until they also are reduced into chyme, or until all that is digestible has passed out. The action of these fibres is often seen in the contracted state of the pyloric portion of the stomach after death, when it alone is contracted and firm, while the cardiac portion forms a dilated sac. Sometimes, by a predominant action of strong circular fibres placed between the cardia and pylorus, the two portions, or ends as they are called, of the stomach, are separated from each other by a kind of hour-glass contraction.

These actions of the stomach are peculiar to it and independent. But it is, also, adapted to act in concert with the abdominal muscles, in certain circumstances which can hardly be called abnormal, as in vomiting and eructation. It has indeed been frequently stated that the stomach itself is quite passive during vomiting, and that the expulsion of its contents is effected solely by the pressure exerted upon it when the capacity of the abdomen is diminished by the contraction of the diaphragm and abdominal muscles: and this opinion has been especially supported by M. Magendie (xxxii. p. 554). After having injected tartar emetic into the veins of dogs, and in other instances given it by the mouth, he states that he never saw the stomach itself contract; and that if in such

cases he drew the stomach out of the abdominal cavity, vomiting was prevented until he returned the viscus to its natural situation, when vomiting immediately ensued. M. Lépine, too, mentions a case in which a patient's abdomen was torn open by a horn, and the stomach wholly protruded: no movements of the exposed organ ensued, and no vomiting until the stomach was returned into the abdominal cavity (lv. vol. ix. p. 147). Magendie also found that pressure with the hand had the same influence as the abdominal muscles; and even the action of the diaphragm alone, pressing against the linea alba, was sufficient to produce vomiting when the abdominal muscles had been cut away. When the stomach was removed, and a pig's bladder was connected with the œsophagus in its stead, vomiting was produced in the same way as when the stomach itself remained uninjured. The latter observation, however, only proves, that the pressure exerted by the contracting abdominal muscles upon an unresisting bag, is sufficient to expel its contents. And the others do not shew more than that a considerable share in the act of vomiting is exercised by the abdominal muscles.

On the other hand, there is reason to believe that the stomach takes some part in the expulsion of its own contents. Facts are wanting to demonstrate this with certainty, though some of the cases of fistulous opening into the stomach seem to support such a view. Moreover, during vomiting, the contraction of the stomach can usually be distinctly felt by the patient; though, at least in animals t appears to be often so slight and quick, that even when the stomach is exposed, its occurrence may be overlooked.

Besides probably taking this share by its contraction, the stomach also essentially contributes to the act of vomiting, by the relaxation of the oblique fibres around the cardiac orifice, coincidently with the contraction of the abdominal muscles and of the rest of its own fibres. For, until the relaxation of these fibres, no vomiting can ensue; when contracted, they can as well resist all the force of the contracting abdominal

and other muscles, as the muscles by which the glottis is closed can resist the same force in the act of straining. Doubtless we may refer many of the acts of retching and ineffectual attempts to vomit to the want of concord between the relaxation of these muscles and the contraction of the rest.

The muscles with which the stomach co-operates in contraction during vomiting, are chiefly and primarily those of the abdomen; the diaphragm also acts, but not as the muscles of the abdominal walls do. They contract and compress the stomach more and more towards the back and upper parts of the diaphragm; and the diaphragm (which is usually drawn down in the deep inspiration that precedes each act of vomiting) holds itself fixed in contraction, and presents an unyielding surface against which the stomach may be pressed. It is enabled to act thus, and probably only thus, because the inspiration which precedes the act of vomiting, is terminated by closure of the glottis; after which the diaphragm can neither descend further, except by expanding the air in the lungs; nor, except by compressing the air, ascend again until, the act of vomiting having ceased, the glottis is opened again.

Some persons possess the power of vomiting at will, without applying any undue irritation to the stomach, but simply by a voluntary effort. It seems also, that this power may be acquired by those who do not naturally possess it, and by continual practice may become a habit. Cases are also of no rare occurrence in which persons habitually swallow their food hastily, and nearly unmasticated; and then, at their leisure, regurgitate it, piece by piece, into their mouth, remasticate, and again swallow it, exactly as is done by the ruminant order of Mammalia.

### *Influence of the Nervous System on Gastric Digestion.*

This influence is manifold; and is evidenced, 1st, in the sensations which induce to the taking of food; 2nd, in the secretion of the gastric fluid; 3rd, in the movements of the food in and from the stomach.

The *sensation of hunger* is manifested in consequence of deficiency of food in the system. The mind refers the sensation to the stomach; yet since the sensation is relieved by the introduction of food either into the stomach itself, or into the blood through other channels than the stomach, it would appear not to depend on the state of the stomach alone. This view is confirmed by the fact, that the division of both pneumogastric nerves, which are the principal channels by which the mind is cognisant of the condition of the stomach, does not appear to allay the sensations of hunger (Reid, lxxiii. vol. iii. p. 899; and Bernard ccxiv. July 7, 1860.)

But that the stomach has some share in this sensation is proved by the relief afforded, though only temporarily, by the introduction of even non-alimentary substances into this organ. It may, therefore, be said that the sensation of hunger is derived from the system generally, but chiefly from the condition of the stomach; the nerves of which, we may suppose, are more affected by the state of the insufficiently replenished blood than those of other organs are.

*The sensation of thirst,* indicating the want of fluid, is referred to the fauces, although, as in hunger, this is merely the local declaration of a general condition existing in the system. For thirst is relieved for only a very short time by washing the dry fauces; but may be relieved completely by the introduction of liquids into the blood, either through the stomach, or by injections into the blood-vessels, or by absorption from the surface of the skin, or the intestines. The sensation of thirst is perceived most naturally whenever there is a disproportionately small quantity of water in the blood: as well, therefore, when water has been abstracted from the blood, as when saline, or any solid matters have been abundantly added to it. We can express the fact (even if it be not an explanation of it), by saying that the nerves of the mouth and fauces, through which the sense of thirst is chiefly derived, are more sensitive to this condition of the blood than other nerves are. And the cases of hunger and thirst are not the only ones in which the mind

derives, from certain organs, a peculiar predominant sensation of some condition affecting the whole body. Thus, the sensation of the "necessity of breathing," is referred especially to the lungs; but, as Volkmann's experiments show, it depends on the condition of the blood which circulates everywhere, and is felt even after the lungs of animals are removed; for they continue, even then, to gasp and manifest the sensation of want of breath. So perhaps, it may be added, the disordered blood in fever, and in other affections of the blood, circulates everywhere, but produces peculiar sensations in only certain parts. And, as with respiration, when the lungs are removed, the mind may still feel the body's want of breath; so in hunger and thirst, even when the stomach has been filled with innutritious substances, or the pneumogastric nerves have been divided, and the mouth and fauces are kept moist, the mind is still aware, by the more obscure sensations in other parts, of the whole body's need of food and water.

The *influence of the nervous system on the secretion of gastric fluid,* is shown plainly enough in the influence of the mind upon digestion in the stomach; and is, in this regard, well illustrated by several of Dr. Beaumont's observations. M. Bernard also, watching the act of gastric digestion in dogs which had fistulous openings into their stomachs, saw that on the instant of dividing their pneumogastric nerves, the process of digestion was stopped, and the mucous membrane of the stomach, previously turgid with blood, became pale, and ceased to secrete. These, however, and the like experiments showing the instant effect of division of the pneumogastric nerves, may prove no more than the effect of a severe shock, and the fact that influences affecting digestion may be conveyed to the stomach through those nerves. From other experiments it may be gathered, that although, as in M. Bernard's, the division of both pneumogastric nerves always temporarily suspends the secretion of gastric fluid, and so arrests the process of digestion, and is occasionally followed by death from inanition; yet the digestive powers of the stomach may be completely

restored after the operation, and the formation of chyme and the nutrition of the animal may be carried on almost as perfectly as in health (Reid, lxxiii. vol. iii. p. 900, and Hübbenet, cxciv.).

It has been said, that after the division of the pneumogastric nerves, the absorption of poisons by the stomach does not take place, or is more slowly effected. But in thirty experiments on Mammalia, which M. Wernscheidt performed under Müller's direction not the least difference could be perceived in the action of narcotic poisons introduced into the stomach, whether the pneumogastric had been divided on both sides or not, provided the animals were of the same species and size. It appears, however, that such poisons as are capable of being rendered inert by the action of the gastric fluid, may, if taken into the stomach shortly after division of both pneumogastric nerves, produce their poisonous effects, in consequence, apparently, of the temporary suspension of the secretion of gastric fluid. Thus, in one of his experiments, M. Bernard gave to each of two dogs, in one of which he had divided the pneumogastric nerves, a dose of emulsine, and half an hour afterwards a dose of amygdaline, substances which are innocent alone, but when mixed produce hydrocyanic acid. The dog whose nerves were cut, died in a quarter of an hour, the substances being absorbed unaltered and mixing in the blood; in the other, the emulsine was decomposed by the gastric fluid before the amygdaline was administered; therefore, hydrocyanic acid was not formed in the blood, and the dog survived. The results of these experiments have been confirmed by Frerichs (xv. art. *Verdauung*).

The influence of the pneumogastric nerves over the secretion of gastric fluid has been of late even more decidedly shewn by M. Bernard, who found that galvanic stimulus of these nerves excited an active secretion of the fluid, while a like stimulus applied to the sympathetic nerves issuing from the semilunar ganglia, caused a diminution and even complete arrest of the secretion (ccxiv., August, 1860).

*The influence of the nervous system on the movements of the stomach* has been often seen in the retardation or arrest of these movements after division of the pneumogastric nerves. The results of irritating the same nerves were ambiguous; but the experiments of Longet (cxxxvi. vol. i. p. 323) and Bischoff, (lxxx. 1848, *Jahresbericht*, p. clv.) have shown that the different results depended on whether the stomach were digesting or not at the time of the experiment. In the act of digestion, the nervous system of the stomach appears to participate in the excitement which prevails through the rest of its organization, and a stimulus applied to the pneumogastric nerves is felt intensely, and active movements of the muscular fibres of the stomach follow; but in the inaction of fasting, the same stimulus produces no effect. So, while the stomach is digesting, the pylorus is too irritable to allow anything but chyme to pass; but when digestion is ended, the undigested parts of the food, and even large bodies, coins, and the like, may pass through it.

### CHANGES OF FOOD IN THE INTESTINES.

In the intestines, the passage of the chyme into which, has been just described, the food, thus far acted on and digested, is exposed to the influence of the bile, the pancreatic fluid, and the secretions of the several glands imbedded in, and forming, the intestinal mucous membrane. By the action of these various secretions, the chyme undergoes further changes; after which, being more perfectly separated from the innutritious parts of the food, it is absorbed by the blood-vessels and lacteals; the rest of the food, with portions of the above-named secretions, is ejected in fæces.

#### *Structure and Secretions of the Intestines.*

The intestinal canal is divided into two chief portions named, from their differences in diameter, the *small* and the *large* intestine, and separated from each other by a mus-

cular valvular structure, the ileo-cæcal valve. This distinction is much less marked in Carnivora than in Herbivora; the large intestine in the latter class of animals being very wide and long. The small intestine, for convenience of description, has been further divided into three portions, viz., the *duodenum*, which extends for eight or ten inches beyond the pylorus; the *jejunum*, which occupies two-fifths, and the *ileum*, which occupies three-fifths of the rest of this portion of the canal. The large intestine also, is subdivided into three portions, viz., the *cæcum*, a short, wide pouch, separated from the small intestines by the *ileo-cæcal* valve; the *colon*, which occupies the principal part of the large intestine, and is divided into an ascending, transverse, and descending portion; and the rectum, which terminates at the anus. The cæcum is said to be absent in all animals which hybernate: it is small in Carnivora, and very large and long in the Solidungula, Ruminantia, and Rodentia, in which there is reason to believe that it takes an especially active part in the digestion of the food which has not been perfectly transformed in the stomach.

The intestines, like the stomach, are constructed of three principal coats, viz., the serous, muscular, and mucous. The fibres of the muscular coat of the small intestine, are arranged in two layers; those of the outer layer being disposed longitudinally; those of the inner layer transversely, or in portions of circles encompassing the canal. In the cæcum and colon, besides those longitudinal fibres, which, as in the small intestines, are thinly disposed on all parts of the walls, others are collected into three strong bands, which are so connected with the other coats of the intestine, especially with the peritoneal coats, that they hold the canal in folds bounding intermediate sacculi. At the rectum, the fasciculi of these longitudinal bands, or *ligaments* of the colon as they are called, spread out and mingle with the other longitudinal fibres, forming with them a thicker layer of longitudinal fibres than exists on any other part of the intestinal canal.

The *mucous membrane* of the small intestine has its surface

greatly extended by being formed in transverse folds, termed *valvulæ conniventes*. These commence in the duodenum, are largely developed therein directly beyond the orifice of the bile-duct, and, retaining the same large size and closely placed, are continued through the whole of the jejunum, and then, gradually diminishing in size and closeness of juxtaposition, they cease near the middle of the ileum. No similar folds exist in any part of the large intestine.

Between the mucous and muscular coats, there occurs a layer of submucous tissue, in which numerous blood-vessels and a rich plexus of nerves and ganglia are imbedded (Meissner, xxxiii. 2nd Ser. vol. 8.)

In the substance of the mucous membrane, numerous *glands* are imbedded; its surface is studded with minute processes termed *villi;* and it is covered throughout with cylindrical *epithelium.*

The *glands of the small intestine* are of three principal kinds, named, after their describers, the glands of Lieberkühn (lxxv.) of Peyer (lxxvi.) and of Brunn or Brunner (lxxvii.) The *glands* or *follicles of Lieberkühn* are simple tubular depressions of the intestinal mucous membrane, thickly distributed over the whole surface both of the large and small intestines.* In the small intestine, these are visible only with the aid of a lens; and their orifices appear as minute dots scattered between the villi. They are larger in the large intestine, and increase in size the nearer they approach the anal end of the intestinal tube; and in the rectum their orifices may be visible to the naked eye. Each tubule or follicle is constructed of the same essential parts as the intestinal mucous membrane, viz., a fine structureless *mem-*

*Fig.* 23.

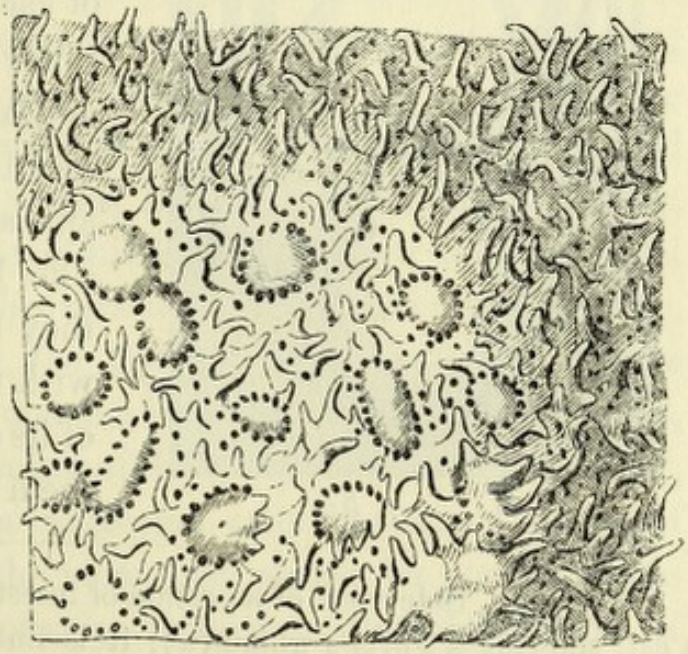
* Lieberkühn only described them as existing in the small intestine; Boehm (lxxvii.) first pointed out their existence over the whole extent of the large intestine also.

*brana propria*, or basement membrane, a layer of cylindrical epithelium lining it (fig. 23), and capillary blood-vessels covering its exterior. Their contents appear to vary, even in health; the varieties being dependent, probably, on the period of time in relation to digestion at which they are examined. At the bottom of the follicle the contents usually consist of a granular material, in which a few cytoblasts or nuclei are imbedded: these cytoblasts, as they ascend towards the surface, are supposed to be gradually developed into nucleated cells, some of which are discharged into the intestinal cavity. The purpose served by the material secreted by these glands is still doubtful. Their large number and the extent of surface occupied by them, seem, however, to indicate that they are concerned in other and higher offices than the mere production of fluid to moisten the surface of the mucous membrane.

The *glands of Peyer* occur exclusively in the small intestine. They are found in greater abundance the nearer to the ileo-cæcal valve. They are met with in two conditions, viz., either

*Fig.* 24.*

*Fig.* 25.†

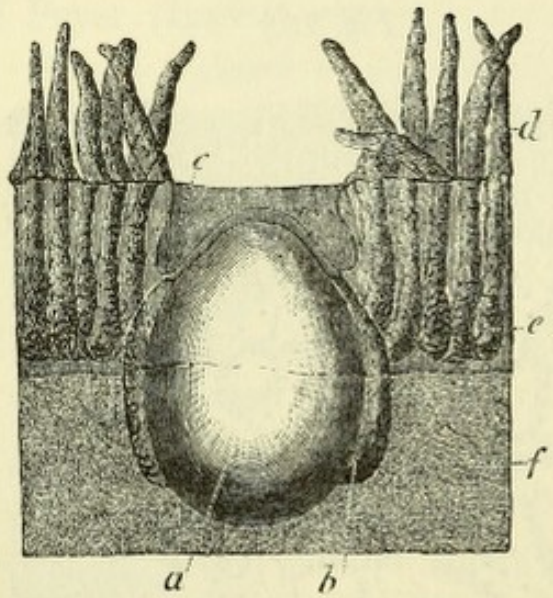


* Fig. 24. Solitary gland of small intestine, after Boehm.

† Fig. 25. Part of a patch of the so-called Peyer's glands magnified, showing the various forms of the sacculi, with their zone of foramina. The rest of the membrane marked with Lieberkühn's follicles, and sprinkled with villi. After Boehm.

scattered singly, in which case they are termed *glandulæ solitariæ*, or aggregated in groups of various sizes, chiefly of an oval form, and situated opposite the attachment of the mesentery. In this state, they are named *glandulæ agminatæ*, the groups being commonly called *Peyer's patches*. In structure, and probably in function, there is no essential difference between the solitary glands and the individual bodies of which each group or patch is made up; but the surface of the solitary glands (fig. 24) is beset with villi, from which those forming the agminate patches (fig. 25) are usually free. In the condition in which they have been most commonly examined, each gland appears as a circular, opaque-white sacculus, from half a line to a line in diameter and, according to the degree in which it is developed, either sunk beneath, or more or less prominently raised on, the surface of a depression or fossa in the mucous membrane. Each gland is surrounded by openings like those of Lieberkühn's follicles (see fig. 25), except that they are more elongated ; and the direction of the long diameter of each opening is such, that the whole produce a radiated appearance around the white sacculus. These openings appear to belong to tubules like Lieberkühn's follicles: they have no communication with the sacculus, and none of its contents escape through them on pressure. Neither

*Fig.* 26.*




* Fig. 26. Side-view of a portion of intestinal mucous membrane of a cat, showing a Peyer's gland (*a*): it is imbedded in the submucous tissue (*f*), the line of separation between which and the mucous membrane passes across the gland: *b*, one of the tubular follicles, the orifices of which form the zone of openings around the gland: *c*, the fossa in the mucous membrane: *d*, villi: *e*, follicles of Lieberkühn. After Bendz (lxxix.).

can any permanent opening be detected in the sacculus or Peyer's gland itself (see fig. 26.)

According to Henle's view, each of these glands is to be regarded as a secreting cell which, when its contents are fully matured, forms a communication with the cavity of the intestine by the absorption or bursting of its own cell-wall, and of the portion of mucous membrane over it; thus it discharges its secretion into the intestinal tube. A small shallow cavity or space remains, for a time, after this absorption or dehiscence, but shortly disappears, together with all trace of the previous gland.

According to Brücke (clxxxix. Nov. 1850), Virchow (ccxxxiii. p. 173), Heidenheim, and others, however, these bodies should not be regarded as temporary gland-cells, which thus discharge their elaborated contents into the intestines, but as analogous to absorbent glands, their probable office being to take up certain materials from the chyle, elaborate and subsequently discharge them into the lacteals, with which they are evidently closely connected; for Brücke has been able to inject the glands through these vessels, and Kölliker observes, that the number of the chyle-vessels coming from the Peyerian patches during the period of digestion is greater than at other parts of the intestine, although the villi found upon them are fewer and less developed (ccxviii. p. 334, 1860). According to this view, Peyer's glands constitute a kind of appendage to the lacteal system, analogous to the mesenteric and lymphatic glands, and have no share in the production of any part of the intestinal fluid. The opaque-white contents of the glands, consist of minute granules of fatty and albuminous matter, mingled with which are nucleated cells in various stages of development; and, if the view just stated be correct, these cells are, no doubt, actively engaged in the elaboration of material destined to be conveyed away by the lacteals.

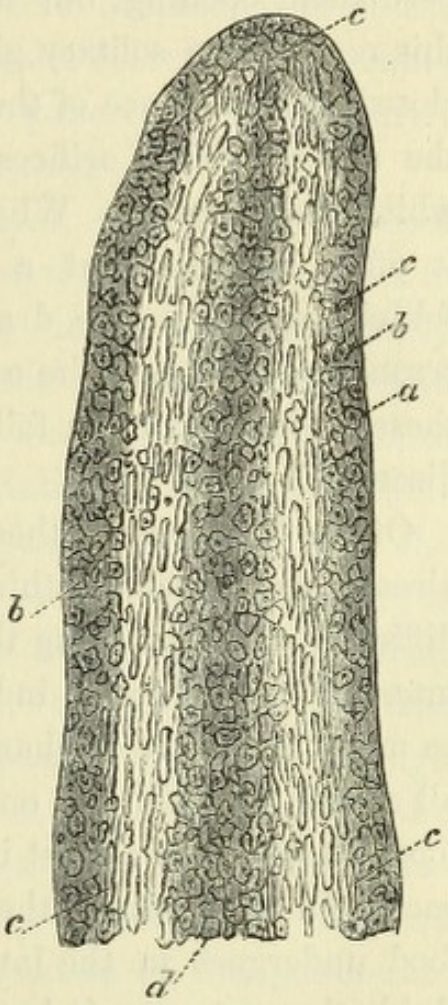
*Brunner's glands* are confined to the duodenum; they are most abundant and thickly set at the commencement of this portion of the intestine, diminishing gradually as the duode-

num advances. They are situated beneath the mucous membrane, imbedded in the submucous tissue, minutely lobulated bodies, visible to the naked eye, like detached small portions of pancreas, and provided with permanent gland-ducts, which pass through the mucous membrane and open on the internal surface of the intestine. As in structure, so probably in function, they resemble the pancreas; or at least stand to it in a similar relation to that which the small labial and buccal glands occupy in relation to the larger salivary glands, the parotid and sub-maxillary.

The *Villi* are confined exclusively to the mucous membrane of the small intestine. They are minute vascular processes, from a quarter of a line to a line and two-thirds in length (Müller, xxxii. p. 285), covering, in the proportion of about twenty-five on every square line, the surface of the mucous membrane (Lieberkühn, lxxv.), and giving it a peculiar velvety, fleecy appearance. They vary in form even in the same animal, and differ according as the vessels they contain are empty or full of chyle; being usually, in the former case, flat and pointed at their summits, in the latter cylindrical or clavate. Into the base of each villus there enter one or more lacteal vessels, which pass up the middle, and extend nearly to the tip, where they terminate either by a closed and somewhat dilated extremity, or by forming a kind of network (see plate 1, fig. 9); in no case do they terminate in perforated or open extremities. (Krause, lxxx. 1837; Valentin, lxxx. 1839; E. H. Weber, lxxx. 1847, p. 400; Kölliker, ccvi. p. 404; and ccxii.) Two or more minute arteries are distributed within each villus; and, from their capillaries, which form a dense network, proceed one or two small veins, which pass out at the base of the villus (see fig. 12, p. 120). Another important constituent of the villus has lately been discovered, namely, a layer of organic muscular fibres, which forms a kind of thin hollow cone immediately around the central lacteal, and is therefore situated beneath the blood-vessels and much of the granular basis of the villus. The addition of acetic acid to

the villus brings out the characteristic nuclei of the muscular fibres, and shews the size and position of the layer most distinctly (fig. 27). Its use is still unknown, though it is impossible to resist the belief, that it is instrumental in the propulsion of chyle along the lacteals. Kölliker has lately shewn that this layer is continuous with a layer of organic muscular fibres situated within the mucous membrane (ccxviii. 1860. p. 327). No nervous elements have been found in the villi.

*Fig.* 27.*




Being a process of the mucous membrane, each villus possesses an investing basement-membrane, the outer surface of which is covered with a layer of cylindrical epithelium, similar to that which invests every other part of the intestinal mucous membrane, and lines the tubular follicles of Lieberkühn.

The office of the villi is the absorption of chyle from the completely digested food in the intestines. The mode in which they effect this will be considered in the chapter on Absorption.

The *glands of the large intestine* are of two kinds, viz., the tubular follicles of Lieberkühn already described, and certain *solitary* glands which are scattered over the whole length of

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* Fig. 27. Intestinal villus of a kitten, deprived of epithelium, treated with acetic acid, and magnified 350 diameters: *a*, basement membrane: *b*, subjacent nuclei: *c*, nuclei of the organic muscular fibres: *d*, roundish nuclei in the centre of the villus. After Kölliker.

this part of the intestines, but are most numerous in the cæcum and its vermiform appendix. Boehm described these solitary glands as simple flask-shaped cavities, provided with a permanent orifice at the apex of the cavity. But Dr. Baly (lxxi. March, 1847) has shown that they have not always a permanent opening, but are sometimes closed, resembling in this respect the solitary glands of the small intestine. When closed, the existence of these glands can only be recognised by the absence of the orifices of the tubular follicles at the spots which they occupy. When a gland is emptied of its contents, it often happens that a number of the adjoining tubular follicles appear to be drawn inwards, and present a radiated arrangement around the centre of the gland. In the midst of these radiating tubular follicles the orifice of the gland may be discerned.

Of the functions of these intestinal glands, as of the others already mentioned, nothing is known with certainty. The difficulty of determining the function of any single set of the intestinal glands must, indeed, seem almost insuperable while so many fluids are discharged together into the intestine: for all acting, probably, at once, produce a general effect upon the food, so that it is almost impossible to discern the share of each. On this ground, the description of the changes that the food undergoes in the intestines must be deferred till all the fluids that act upon it have been described.

### *The Pancreas, and its Secretion.*

The pancreas is situated within the curve formed by the duodenum; and its main duct opens into that intestine, either through a small opening or through a duct common to itself and to the liver. The pancreas, in its minute anatomy, closely resembles the salivary glands; and the fluid elaborated by it appears almost identical with saliva. When obtained pure, in all the different animals in which it has been hitherto examined, it has been found colourless, transparent, and slightly viscid. The most recent investigations tend to confirm the

account given by Leuret and Lassaigne, that when fresh it is alkaline, and contains a peculiar animal matter, named *pancreatine*, and certain salts, both of which are very similar to those found in saliva, except in that there is no sulphocyanogen. Pancreatine is a substance coagulable by heat, and in many other respects very like albumen: to it the peculiar digestive power of the pancreatic secretion is probably due (Bernard). Like saliva, the pancreatic fluid shortly after its escape, becomes neutral and then acid.

Numerous experiments have shewn, that *starch* is acted upon by the pancreatic fluid, or by portions of pancreas put in starch-paste, in the same manner as, though more powerfully than, it is by saliva and portions of the salivary glands. And although, as before stated (p. 202), many substances besides those glands can excite the transformation of starch into dextrine and grape sugar, yet it appears probable that the pancreatic fluid, exercising this power of transformation, is largely subservient to the purpose of digesting starch. MM. Bouchardat and Sandras (xix. Jan., 1845) have shewn that the raw starch-granules which have passed unchanged through the crops and gizzards of granivorous birds, or through the stomachs of herbivorous Mammalia, are, in the small intestine, disorganised, eroded, and finally dissolved, as they are when exposed, in experiment, to the action of the pancreatic fluid. The bile cannot effect such a change in starch; but it remains yet to be proved whether the pancreas or the intestinal mucous membrane has the greater share in it, for the secretions of both seem to possess the power of converting the starch into sugar.

The existence of a pancreas in Carnivora, which have little or no starch in their food, and the results of various observations and experiments, leave very little doubt that the pancreatic secretion also assists largely in the digestion of *fatty matters*, by transforming them into a kind of emulsion, and thus rendering them capable of absorption by the lacteals. Numerous cases are recorded in which the pan-

creatic duct being obstructed so that the secretion could not be discharged, fatty or oily matter was abundantly discharged from the intestines (xli. vol. xviii. p. 57.) In nearly all these cases, indeed, the liver was coincidently diseased, and the change or absence of the bile might appear to contribute to the result ; yet the frequency of extensive disease of the liver, unaccompanied by fatty discharges from the intestines, favours the view that, in these cases, it is to the absence of the pancreatic fluid from the intestines that the excretion or non-absorption of fatty matter should be ascribed. In Bernard's experiments, too, fat always appeared in the evacuations when the pancreas was destroyed, or its duct tied. Bernard, indeed, is of opinion that to emulsify fat is the express office of the pancreas, and the evidence that he and others have brought forward in support of this view is very weighty (see especially ccxvii.) At the same time, however, it must be remembered, that the experiments of Lenz (cxcvi.), Frerichs (xv., art. *Verdauung*), and many others shew that other secretions in the intestinal canal besides the pancreatic possess the power of emulsifying fat. For example, they tied the pancreatic duct in cats, and after keeping them fasting for some time, to allow of the entire removal of the pancreatic fluid which might have passed into the intestine, they fed them with milk and fat meat, and found on killing them and opening their intestinal canal, that the lacteals were filled with ordinary milky chyle. Moreover, in young dogs, Frerichs applied a ligature around the upper part of the small intestine below the entrance of the pancreatic duct, and then injected milk and oil into the lower part of the intestine, and found that the oily matters were completely absorbed by the lacteals. The power of emulsifying fat, therefore, although perhaps mainly exercised by the secretion of the pancreas, is evidently possessed also by other secretions poured into the intestines. The influence of the bile in this respect is strongly maintained by some.

From the experiments of Bidder and Schmidt, Frerichs

and others, it would appear that the pancreatic secretion has no solvent action on *albuminous* substances. Yet more recent experiments made by Lucien Corvisart (lix. 1859, p. 39) yield an opposite result, and seem to prove that the digestive power of this secretion over albuminous substances is almost as great as that of the gastric fluid, converting them with almost equal readiness into peptone. His conclusions are, to a certain extent, confirmed by Dr. Harley (cxc., 1860) and others; but opposed by Dr. Brinton, who, whilst admitting that infusions of the pancreas have the power of dissolving coagulated albumen, believes that this power is chiefly associated with putrefaction, and that during life the healthy secretion of this gland has probably no specific digestive power over albuminous substances (cxvi., Aug., 1859). Dr. Brinton's objections, as well as those of Keferstein, have been answered by Corvisart, who still adheres to his opinion (xxxiii., 1859, p. 119, and cxvi., Feb., 1860). This part of the subject, therefore, as well as many others relating to the chemistry of digestion, must be considered as still unsettled.

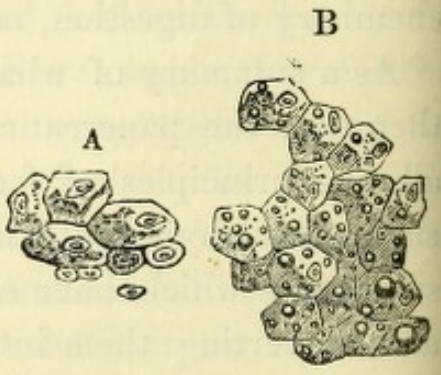
As a summary of what has been just said, it would appear then that the pancreatic secretion is capable of acting upon all the principles of food, readily transforming starch into sugar, emulsifying fat, and, perhaps, dissolving the albuminous substances which have escaped the action of the gastric fluid, and converting them into peptone. The relative share, however, which it takes in these several processes is still the subject of discussion.

### *The Liver and its Secretion.*

*Structure of the Liver.*—The liver receives blood through two vessels, the hepatic artery and the portal vein. The former, conveying arterial blood, appears to be destined chiefly for the nutrition of the coats of the large vessels, the ducts, and the investing membranes belonging to the liver, supplying these parts with blood as the bronchial artery does

the corresponding parts in the lungs (see p. 158). Through the latter, which carries venous blood, are supplied the materials for the formation of bile.

The tributary branches, by the convergence and junction of which the main trunk of the portal vein is formed, comprise the veins which receive the blood from the stomach and intestinal canal, the spleen, pancreas, and gall-bladder. The trunk thus formed branches, like an artery, in the liver, and its minutest divisions (short of the capillaries) are so arranged that they divide, or, as it were, map out, the whole liver into minute nearly oval portions or lobules, from $\frac{1}{40}$th to $\frac{1}{20}$th of an inch in diameter. From these *interlobular veins* (as they are called) proceed on every side minute capillaries, which form dense net-works that seem to make up nearly the whole substance of the lobules. Through the capillaries, the blood passes into *intra-lobular veins,* of which one with its outspread branches, occupies the centre, or axis of each lobule; and these intra-lobular veins, by successive junction and conflux, make up the trunks of the hepatic veins, by which the blood of the portal vein, after secreting the bile, is carried from the liver. The interspaces left in the plexuses of capillaries in every lobule of the liver appear to be filled with nucleated cells (hepatic or bile-cells, fig. 28, A). These are rounded or polygonal cells, from $\frac{1}{800}$th to $\frac{1}{1000}$ of an inch in diameter, containing well-marked nuclei and granules, and having, sometimes, a yellowish tinge, especially about their nuclei, derived from the bile, which appears to be first formed in them; frequently they contain various-sized particles of fat (B, fig. 28), though this fatty matter is probably not one of the natural constituents of healthy cells. In what relation these cells stand to the minutest bile-ducts is still unsettled; according to some observers, they form or line ducts, arranged in



plexuses like those of the capillary blood-vessels, and interlacing with them (Kiernan, xliii. 1833, Kronenberg, lxxx. 1844, E. H. Weber, lxxx. 1844, Backer, cxlvi., Retzius, lxxx. 1850, Lionel Beale, cxxiii. 1856, p. 454, and ccxxvi); but, according to others, they are only *packed in* among the blood-vessels, and by temporary communications discharge their contents into the minute bile-ducts which line the spaces between the lobules, and never enter within them (Henle, xxxvii., Handfield Jones, lxxi. vol. xxxix. p. 387, and xliii. 1846—9, and 1853, Kölliker, ccvi. p. 418, and ccxviii. 1860, p. 343).*

The blood which the portal vein conveys to the liver is supplied from two chief sources; namely, that in the gastric and mesenteric veins, which contains the soluble elements of food absorbed from the stomach and intestines during digestion, and that in the splenic vein: it must, therefore, combine the qualities of the blood from each of these sources. The blood from the gastric and mesenteric veins will vary much according to the stage of digestion and the nature of the food taken, and can therefore seldom be exactly the same. The blood from the splenic vein is probably more definite in composition, though also liable to alterations according to the stage of the digestive process and other circumstances. Speaking generally,—and without considering the sugar, dextrine, and other soluble matters which may have been absorbed from the alimentary canal,—the blood in the gastric and mesenteric veins appears to be deficient in solid matters, especially in red corpuscles, owing to dilution by the quantity of water absorbed, to contain an excess of albumen, though chiefly of a lower kind than usual, resulting from the digestion of nitrogenised substances, and termed albuminose (p. 224), and to yield a less tenacious kind of fibrine than that of blood

* On the structure of the Liver, the student may advantageously read the original papers of Kiernan (xliii. 1833, and lxxi. vol. xv.), or the description in Dr. Budd's Treatise on Diseases of the Liver, as well as the more modern accounts referred to in the text.

generally. The blood of the splenic vein seems generally to be deficient in red corpuscles, and to contain an unusually large proportion of albumen: the fibrine seems to vary in relative amount, being sometimes more, sometimes less, but like that in the mesenteric veins, it is said to be deficient in tenacity. The quantity of solid matter is, by some observers, said to be much reduced, by others to be scarcely below the average. The blood of the portal vein, combining the peculiarities of its two factors, the splenic and mesenteric venous blood, is usually of lower specific gravity than blood generally, is more watery, contains fewer red corpuscles, more albumen, chiefly in the form of albuminose, and yields a less firm clot than that yielded by other blood, owing to the deficient tenacity of its fibrine. These characteristics of portal blood refer to the composition of the blood itself, and have no reference to the extraneous substances, such as the absorbed materials of the food which it may contain; neither, indeed, has any complete analysis of these been given.

Comparative analyses of blood in the portal vein and blood in the hepatic veins have also been frequently made, with the view of determining the changes which this fluid undergoes in its transit through the liver. Great diversity, however, is observable in the analyses of these two kinds of blood by different chemists. Part of this diversity is no doubt attributable to the fact pointed out by Bernard, that unless the portal vein is tied before the liver is removed from the body, hepatic venous blood is very liable to regurgitate into the portal vein, and thus vitiate the result of the analysis. Guarding against this source of error, recent observers seem to have determined that hepatic venous blood contains less water, albumen, and salts, than the blood of the portal vein; but that it yields a much larger amount of extractive matter, in which is one constant element, namely, grape-sugar, which is found equally the same, whether saccharine or farinaceous matter have been present in the food or not.*

* For the latest observations on the composition of the portal and

The *Secretion of Bile,* of which we will now speak, is the most obvious, and one of the chief functions which the liver has to perform; but, as will be presently shewn, it is not the only one; for recent discoveries have shewn that important changes are effected in certain constituents of the blood in its transit through this gland whereby they are rendered more fit for their subsequent purposes in the animal economy.

*Composition of the Bile.*—The bile is a somewhat viscid fluid, of a yellow or greenish-yellow colour, a strongly bitter taste, and a peculiar nauseous smell; its specific gravity is from 1026 to 1030. Its colour and degree of consistence vary much, apparently independent of disease; but, as a rule, it becomes gradually more deeply coloured and thicker while it advances along its ducts, or remains long in the gall-bladder, wherein, at the same time, it becomes more viscid and ropy from being mixed with the mucus.

The bile has been always described as having naturally a slightly alkaline reaction; but the investigations of Gorup-Besanez (lxxxii.), and Bidder and Schmidt (ccviii.), shew that in man, oxen, and pigs, it is always, when first secreted, exactly neutral; but, in the early stages of its decomposition, is apt to become acid, and subsequently alkaline.

Numerous analyses of the bile of man and animals have been published; that of the bile of the ox by Berzelius (xv. art. *Galle*, p. 518), is perhaps one of the most correct, and the researches of Gorup-Besanez, Strecker, and others, shew that the composition of human bile is essentially similar. The analysis by Berzelius gives—

| | |
|---|---|
| Water . . . . . | 904·4 |
| Biline (with fat and colouring principles) . | 80·0 |
| Mucus, chiefly from the gall-bladder . . | 3·0 |
| Salts . . . . . | 12·6 |
| | 1000·0 |

hepatic venous blood, see Scherer's Reports in Canstatt's Jahresbericht, Gray (ccxiii.), Carpenter (ccvii. p. 168), and Lehmann (cciii. and ccxxi.)

The *Biline* or *biliary matter* described by Berzelius, when freed by ether from the fat with which it is combined, is a resinoid substance, soluble in water, alcohol, and alkaline solutions, and giving to the watery solution the taste and general character of bile. Mulder (xiv. 1847), whose account of biline accords very closely with that of Berzelius, describes it as being neutral, and without the tendency to unite with bases, solid but not crystallizable. Berzelius and Mulder both consider biline to be a single substance, which, in decomposition, yields various materials that have been regarded as natural constituents of bile, such as the biliary resin and picromel of Thenard (xiii. t. i. p. 23), the taurine found by Gmelin, the dyslysin, choleic, cholinic, fellinic, and other acids of as many other writers.* According to Mulder, this decomposition of biline begins in the gall-bladder of the living animal, and continues out of the body until the whole of the biline is decomposed; and by reason of its quickness and the variety of its results, the exact composition of pure biline cannot be determined.

According to Lehmann, Strecker, and Bidder and Schmidt, however, biliary matter is not the single substance it was supposed by Berzelius and Mulder to be, but is a compound of soda combined with one or both of two resinous acids, which by Strecker are named cholic and choleic, by Lehmann, glycocholic and taurocholic, because the former consists, he believes, of cholic acid conjugated with glycine (or sugar of gelatine), the latter of the same acid conjugated with taurine. In the bile of most Mammalia, according to Lehmann, both these acids, combined with soda, exist, and constitute about

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* The principal writers on the chemistry of the bile, besides those just quoted, are Kemp, in various parts of the Chemical Gazette and London Medical Gazette; Demarçay (xii. 67, p. 177); Liebig (xi. 3rd. edit.); Prout (xxi. p. 502); Griffith (cii.); Strecker (x. bd. 66, pp. 1—43); Lehmann (cciii. and ccx); Bidder and Schmidt (ccviii.)

75 per cent. of the solid matter. In the dog, there is no glycocholic, but only taurocholic acid united with soda (ccx. p. 157).

The *Fatty matter* of bile consists chiefly of the crystalline substance named cholestearine (see p. 9). Other fatty substances are usually found in various small proportions, such as oleine and margarine, or their acids, oleic and margaric acids, combined with potash and soda.

The *colouring matter* has not yet been obtained pure from the bile, owing to the facility with which it is decomposed. It occasionally deposits itself in the gall-bladder as a yellow substance mixed with mucus, and in this state has been frequently examined. Berzelius (xv. art. *Galle*) gave it the name of *cholepyrrhine* or *bilipyrrhine;* Simon (lxxxii. vol. i. p. 43) named it *biliphæine.* Berzelius thought it composed of two colouring matters, which he called *biliverdin,* and *bilifulvine.* This colouring matter appears to be formed at the liver, and does not pre-exist in the blood. In cases of biliary obstruction, it is often reabsorbed, circulates with the blood, and gives to the tissues the yellow tint characteristic of jaundice.

The *mucus* in bile is derived chiefly from the mucous membrane of the gall-bladder, but in part also from the hepatic ducts and their branches. It constitutes the residue after bile is treated with alcohol. The epithelium with which it is mixed may be detected in the bile with the microscope in the form of cylindrical cells, either scattered or still held together in layers. To the presence of this mucus is probably to be ascribed the rapid decomposition undergone by the biline; for, according to Berzelius, if the mucus be separated, bile will remain unchanged for many days.

The *saline* or *inorganic constituents* of the bile are similar to those found in most other secreted fluids, including the chlorides of sodium and potassium, and the phosphates and sulphates of soda, potash, lime, and magnesia. It has generally been supposed that the bile contains free soda, or an alkaline salt of this substance, such as the carbonate or tribasic phosphate;

but Gorup-Besanez having shown, as already stated, that the bile is really neutral, it is probable that the carbonate and tribasic phosphate of soda, found in the ashes of bile, are formed in the incineration, and do not exist as such in the fluid. Oxide of iron also is a common constituent of the ashes of bile (Gorup-Besanez, lxxxiii.); and copper is generally found in healthy bile, and constantly in biliary calculi (Gorup-Besanez, lxxxiii.: and see p. 19).

Such are the principal chemical constituents of bile; but its physiology is, perhaps, better illustrated by its ultimate elementary composition. According to Liebig's analysis, the biliary matter—consisting of biline and the products of its spontaneous decomposition—yields, on analysis, 76 atoms of carbon, 66 of hydrogen, 22 of oxygen, 2 of nitrogen, and a certain quantity of sulphur.* Comparing this with the ultimate composition of the organic parts of blood—which may be stated at $C_{48}H_{36}N_6O_{14}$ with sulphur and phosphorus—it is evident that bile contains a large preponderance of carbon and hydrogen, and a deficiency of nitrogen. The import of this will presently appear.

*The process of secreting bile* is probably continually going on, but appears to be retarded during fasting, and accelerated on taking food. This was shown by Blondlot (xx. p. 62), who, having tied the common bile-duct of a dog, and established a fistulous opening between the skin and gall-bladder, whereby all the bile secreted was discharged at the surface, noticed

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* The sulphur is combined with the taurine—one of the substances yielded by the decomposition of biline. According to Redtenbacher's analysis (x. Feb. 1846), the general correctness of which is confirmed by Dr. Gregory (vii. p. 566) and others, the quantity of sulphur in taurine is about 26 per cent. According to Dr. Kemp (vi. No. 99, 1846), the sulphur in the bile of the ox, dried and freed from mucus, colouring matter, and salts, constitutes about 3 per cent.

that when the animal was fasting, sometimes not a drop of bile was discharged for several hours; but that, in about ten minutes after the introduction of food into the stomach, the bile began to flow abundantly, and continued to do so during the whole period of digestion. Bidder and Schmidt's observations are quite in accordance with this.

The bile is probably formed first in the hepatic cells; then, being discharged (in some unknown way; perhaps, as Kölliker suggests, by transmission from cell to cell) into the minutest hepatic ducts, it passes into the larger trunks, and from the main hepatic duct may be carried at once into the duodenum.* But, probably, this happens only while digestion is going on; during fasting it flows from the common bile-duct into the cystic duct, and thence into the gall-bladder where it accumulates till, in the next period of digestion, it is discharged into the intestine. The gall-bladder thus fulfils what appears to be its chief or only office, that of a reservoir; for it enables bile to be constantly secreted for the purification of the blood, yet insures that it shall all be employed in the service of digestion, although digestion is periodic, and the secretion of bile is constant.

The mechanism by which the bile passes into the gall-bladder is simple. The orifice through which the common bile-duct communicates with the duodenum, is narrower than the duct, and appears to be closed, except when there is sufficient pressure behind to force the bile through it. The pressure exercised upon the bile secreted during the intervals of digestion, appears insufficient to overcome the force with which the orifice of the duct is closed; and the bile in the common duct, finding no exit into the intestine, traverses the cystic duct, and so passes into the gall-bladder, being probably

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* It should be observed, however, that according to Dr. Handfield Jones, the hepatic cells have little if any share in the secretion of bile, their office being chiefly to form the sugar which the liver contains (xliii. 1853).

aided in this retrograde course by the peristaltic action of the ducts. The bile is discharged from the gall-bladder, and enters the duodenum on the introduction of food into the small intestine: being pressed on by the contraction of the coats of the gall-bladder, and probably of the common bile-duct also; for both these organs contain organic muscular fibre-cells. Their contraction is excited by the stimulus of the food in the duodenum acting so as to produce a reflex movement, the force of which is sufficient to open the orifice of the common bile-duct.

Various estimates have been made of the quantity of bile discharged into the intestines in twenty-four hours : the quantity doubtless varies, like that of the gastric fluid, in proportion to the amount of food taken. The usual estimate has been that, in man, the quantity of bile daily secreted, is from seventeen to twenty-four ounces (xi. 1st. edit. p. 64); but Blondlot's investigations make it probable that this estimate is too high. The quantity discharged through the fistulous opening of the gall-bladder in one of his dogs amounted, on the average, to twelve and a-half drachms in twenty-four hours. And if, with Haller, we suppose that the liver of man secretes from four to five times the quantity secreted by the liver of a dog, this would give from six to eight ounces, as the average quantity of bile poured into the intestinal canal in twenty-four hours (xx. p. 61). On the other hand, however, it must be observed, that Bidder and Schmidt estimate the daily quantity secreted by man at about 54 ounces.

The *purposes served by the secretion of bile*, may be considered to be of two principal kinds, viz., *excrementitious* and *digestive*.

As an excrementitious substance, the bile is destined especially for the preparation of portions of carbon and hydrogen, in order that they may be removed from the blood: and its adaptation to this purpose is well illustrated by the peculiarities attending its secretion and disposal in the fœtus. During intra-uterine life, the lungs and the intestinal canal are almost inactive: there is no respiration of open air or digestion of food;

these are unnecessary, because of the supply of well-elaborated nutriment received by the vessels of the fœtus at the placenta. The liver, during the same time, is proportionally larger than it is after birth, and the secretion of bile is active, although there is no food in the intestinal canal upon which it can exercise any digestive property. At birth, the intestinal canal is full of thick bile, mixed with intestinal secretion; for the *meconium*, or fæces of the fœtus is shown, by the analyses of Simon (lxxxii. vol. ii. p. 367), and of Frerichs (xxii. vol. iii. p. 314) to contain all the essential principles of bile.* In the fœtus, therefore, the main purpose of the secretion of bile must be the purification of the blood by *direct* excretion, *i.e.*, by separation from the blood, and ejection from the body without further change, Probably, all the bile secreted in fœtal life, is incorporated in the meconium, and with it discharged; and thus the liver may be said to discharge a function in some sense vicarious of that of the lungs. For, in the fœtus, nearly all the blood coming from the placenta passes through the liver, previous to its distribution to the several organs of the body; and the abstraction of carbon, hydrogen, and other elements of bile will purify it, as in extra-uterine life the separation of carbonic acid and water at the lungs does.

This evident disposal of the fœtal bile by excretion, makes it highly probable that the bile in extra-uterine life is also, at least for the most part, destined to be discharged as excrement. But the analysis of the fæces of both children and adults shows that (except when rapidly discharged in purgation) they contain very little of the bile secreted, probably not more than one-sixteenth part of its weight, and that this portion includes only its colouring, and some of its fatty matters,

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* Analysis of Meconium by Frerichs:—

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|---|---|
| Biliary resin . . . . . | 15·6 |
| Cholestearine, oleine, and margarine . . . | 15·4 |
| Epithelium, mucus, pigment, and salts . . | 69· |
| | 100· |

but none of its essential principle, the biline (Berzelius, xxiv. Gorup-Besanez, lxxxiii. p. 51, Pettenkofer, x. 1844, p. 90, and Bidder and Schmidt, ccviii.). All the biline is again absorbed from the intestines into the blood. But the elementary composition of biline (see p. 252) shows such a preponderance of carbon and hydrogen, that it cannot be appropriated to the nutrition of the tissues; therefore, it may be presumed that after absorption, the carbon and hydrogen of the biline combining with oxygen, are excreted in carbonic acid and water. The destination of the bile is, on this theory, essentially the same in both fœtal and extra-uterine life; only, in the former, it is *directly* excreted, in the latter *indirectly*, being, before final ejection, modified in its absorption from the intestines, and mingled with the blood.

The change from the direct to the indirect mode of excretion of the bile may, with much probability, be connected with a purpose in relation to the development of heat. The temperature of the fœtus is maintained by that of the parent, and needs no source of heat within the body of the fœtus itself; but, in extra-uterine life, there is (as one may say) a waste of material for heat when any excretion is discharged unoxydised: the carbon and hydrogen of the biline, therefore, instead of being ejected in the fæces, are re-absorbed, in order that they may be combined with oxygen, and that in the combination, heat may be generated.

That ejection is the final destination of the bile, and that whatever other purposes it may serve, are not essential to the maintenance of life, appear from facts mentioned by Blondlot (xx.). He found that dogs may live in health for at least several months, even though the bile is prevented from passing into the intestines by removing a portion of the common bile-duct, provided all the bile that is secreted can be discharged from the body, by keeping open a fistulous communication between the skin and the gall-bladder. It must not, however, be thought indifferent, whether the bile be re-absorbed or not, provided it be ejected; for, in experiments similar to

those of Blondlot, Schwann (lxxx. 1844) found that the animals always died with the signs of inanition; such signs, it may be supposed, as would be produced by the deficiency of carbon and hydrogen in the blood.

Though the chief purpose of the secretion of bile may thus appear to be the purification of the blood by excretion, yet there are certain reasons for believing that, while it is in the intestines, it may serve some part in the process of digestion. In nearly all animals, for example, the bile is discharged, not through an excretory duct communicating with the external surface or with a simple reservoir, as most excretions are, but is made to pass into the intestinal canal, so as to be mingled with the chyme directly after it leaves the stomach; an arrangement, the constancy of which clearly indicates that the bile has some important relations to the food with which it is thus mixed. A similar indication is furnished also by the fact that the secretion of bile is more active, and the quantity discharged into the intestines much greater, during digestion, than at any other time (Blondlot xx. p. 62).* Moreover, the bile is a highly elaborated fluid, formed of materials which do not pre-exist in the same condition in the blood, and secreted by cells in a highly organized gland; in which respects it resembles the higher kinds of secretions which are destined to serve some important purposes in the economy, and differs from those which, like carbonic acid and the urine, are straightway discharged from the body.

Respecting the nature of the influence exercised by the bile in digestion, there is, however, very little at present known. It is supposed by some that the bile assists in converting the chyme into chyle, especially by emulsifying the fat, and thus rendering it capable of being absorbed by the lacteals.

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* This activity of secretion during digestion may, however, be in part ascribed to the fact that a greater quanity of blood is sent through the portal vein to the liver at this time, and that this blood contains some of the materials of the food absorbed from the stomach and intestines.

For it has appeared in some experiments in which the common bile-duct was tied, that although the process of digestion in the stomach was unaffected, chyle was no longer well-formed; the contents of the lacteals consisting of clear, colourless fluid, instead of being opaque and white, as they ordinarily are, after feeding (Sir B. Brodie, v. 1823; Tiedemann and Gmelin, xxix; Bidder and Schmidt, ccviii. pp. 215—234).

The general tendency, however, of modern observation is to the effect, that the bile has very little influence on the process of digestion. When mixed, artificially, with the principles of food, and kept at a temperature of 100° Fah., it appears to exert no special action either on albuminous, starchy, or oleaginous substances. Experiments like these, however, made on bile alone and out of the body should be very cautiously received as evidence concerning the digestive function of this fluid when placed under natural conditions, and especially when mixed with the other secretions poured into the intestinal canal. For the observations of Zander (cxcv.) shew very clearly that much more powerful effects are produced on the chyle by these several secretions when mixed than when left to act separately: and it is therefore probably to their combined, rather than to their separate effect, that the most important changes ensuing in the alimentary matters must be ascribed; the share which each takes in the general result being quite unknown. It appears quite certain, however, that the various alimentary substances have, in the salivary, gastric, pancreatic, and intestinal secretions, ample provision for their complete digestion, independent of any action of the bile.

The bile, however, like the gastric fluid, has a strongly antiseptic power, and may serve to prevent the decomposition of food during the time of its sojourn in the intestines. The experiments of Tiedemann and Gmelin shew that the contents of the intestines are much more fetid after the common bile-duct has been tied than at other times; and the experiments of Bidder and Schmidt on animals with an artificial biliary

fistula, confirm this observation; moreover, it is found that the mixture of bile with a fermenting fluid stops or spoils the process of fermentation.

Again, the contents of the small intestine are alkaline, though the chyme is acid. The bile, with the pancreatic fluid, and the secretion of the intestinal glands, is supposed to make this acid fluid alkaline, and the bile was formerly thought to do so by the free soda, or the carbonate or tribasic phosphate of soda, said to be among its inorganic constituents; but, as already stated (p. 249), the bile is neutral, and it is more probable that, as Valentin suggests (iv. vol. i. p. 338), the chyme is made alkaline by the ammonia which is one of the products of the spontaneous decomposition of bile in the intestines.

The bile has also been considered to act as a kind of natural purgative by promoting an increased secretion of the intestinal glands, and by stimulating the intestines to the propulsion of their contents. This view receives support from the constipation which ordinarily exists in jaundice, from the diarrhœa which accompanies excessive secretion of bile, and from the purgative properties of ox-gall.

Nothing is known with certainty respecting the changes which the reabsorbed portions of the bile undergo in either the intestines or the absorbent vessels. That they are much changed appears from the impossibility of detecting them in the blood; and that part of this change is effected in the liver (through which these portions of the reabsorbed bile must pass with all the other materials absorbed from the digestive canal) is probable from an experiment of Magendie who found that when he injected bile into the portal vein the dog was unharmed, but was killed when he injected the bile into one of the systemic vessels.

The secretion of bile, as already observed, is only one of the purposes fulfilled by the liver. Another very important function appears to be that of so acting upon certain consti-

tuents of the blood passing through it, as to render some of them capable of assimilation with the blood generally, and to prepare others for being duly eliminated in the process of respiration. From the labours of M. Bernard, to whom we owe most of what we know on this subject, it appears that the low form of albuminous matter, or albuminose, conveyed from the alimentary canal by the blood of the portal vein, requires to be submitted to the influence of the liver before it can be assimilated by the blood; for if such albuminous matter is injected into the jugular vein, it speedily appears in the urine; but if introduced into the portal vein, and thus allowed to traverse the liver, it is no longer ejected as a foreign substance, but is probably incorporated with the albuminous part of the blood.

An important influence seems also to be exerted by the liver upon the saccharine matters derived from the alimentary canal. The chief purpose of the saccharine and amylaceous principles of food is probably in relation to respiration and the production of animal heat; but in order that they may fulfil this their main office, it seems to be essential that they should undergo some intermediate change, which is effected in the liver, and which consists in their conversion into a peculiar form of saccharine matter, very similar to glucose, or diabetic sugar. That such influence is exerted by the liver seems proved by the fact that when cane sugar is injected into the jugular vein, it is speedily thrown out of the system, and appears in the urine; but when injected into the portal vein, and thus enabled to traverse the liver, it ceases to be excreted at the kidneys: and, what is still more to the point, a very large quantity of glucose may be injected into the venous system without any trace of it appearing in the urine. So that it may be concluded, that the saccharine principles of the food undergo, in their passage through the liver, some transformation necessary to the subsequent purpose they have to fulfil in relation to the respiratory process, and without which, such purpose probably could not be properly accomplished, and the

substances themselves would be eliminated as foreign matters by the kidneys.

Then, again, it has been discovered by Bernard, and the discovery has been amply confirmed by Lehmann and other distinguished animal chemists, that the liver possesses the remarkable property of forming sugar out of principles in the blood which contain no trace of saccharine or amylaceous matter. Sugar appears to be almost as essential in the animal economy, as albumen and fat. If the system be deprived of it, signs of disturbed health and imperfect nutrition speedily appear. In Herbivora and in animals living on mixed diet, a large part of the sugar is derived from the saccharine and amylaceous principles introduced in their food. But in animals fed exclusively on flesh, and deprived therefore of this source of sugar, the liver furnishes the source whence it is obtained. Not only in Carnivora, however, but apparently in all classes of animals the liver is continually engaged, during health, in forming sugar in large amount. This substance may always be found in the liver, even when absent from all other parts of the body.

The researches of Bernard and others, however, have shewn that the sugar is not formed at once at the liver, but that this organ has the power of producing a peculiar ternary substance, very like glucose, which is readily convertible into sugar when in contact with any animal ferment. This substance has received from various chemists the different names of glycose, glycogen, glycogenic substance, glycocene, animal starch, amylon, hepatine. According to Bernard and most other physiologists, its conversion into sugar takes place rapidly during life, and the sugar is conveyed by the blood of the hepatic veins to be consumed in respiration at the lungs. Pavy and others, however, believe that the conversion into sugar only occurs after death, and that during life no sugar exists in healthy livers, the glycogenic substance or hepatine being prevented by some force from undergoing the transformation. The glycogenic substance has been extracted

from the liver, isolated and analysed. It is said to be whitish, tasteless, soluble in water, and to possess the chemical qualities intermediate between those of hydrated starch and dextrine. Its composition is $C_{12}H_{12}O_{12}$. It manifests a remarkable tendency to pass into sugar in presence of any animal ferment, such, for example, as may be found in the blood, urine, saliva, or pancreatic secretion.

Much doubt exists respecting the mode in which this glycogenic substance is formed in the liver, and the materials which furnish its source. Since its quantity is increased after feeding, it is probable that part of it is derived from alimentary principles absorbed from the digestive canal; and since its formation continues even when there is no starch or sugar in the food, the albuminous or fatty principles have been thought capable of furnishing part of it. Numerous experiments, however, having proved that the liver continues to form sugar in animals after prolonged starvation, and during hybernation, and even after death, its production is clearly independent of the elements of food. One of Bernard's experiments may be quoted in proof of this:—Having fed a healthy dog for many days exclusively on flesh, he killed it, removed the liver at once, and before the contained blood could have coagulated, he thoroughly washed out its tissue by passing a stream of cold water through the portal vein. He continued the injection until the liver was completely exsanguined, until the issuing water contained not a trace of sugar or albumen, and until no sugar was yielded by portions of the organ cut into slices and boiled in water. Having thus deprived the liver of all saccharine matter, he left it for twenty-four hours, and on then examining it, found in its tissue a large quantity of soluble sugar, which must clearly have been formed subsequently to the organ being washed, and out of some previously insoluble and non-saccharine substance. This and other experiments led him and others to the conclusion that the formation of sugar by the liver is the result of a kind of secretion or elaboration out of materials

in the solid tissues of the gland—such secretion being probably effected by the hepatic cells, in which, indeed, the glycose has been detected.

According to this view, then, the liver may be regarded as an organ engaged in forming two kinds of secretion, namely, bile and sugar, or rather, the glycogenic substance readily convertible into sugar. The former, chiefly excrementitious, passes along the bile-ducts into the intestines, where it may subserve some purposes in relation to digestion, and is then for the most part re-absorbed, and ultimately eliminated during the processes concerned in the production of animal heat. The latter, namely sugar, being soluble, is taken up by the blood in the hepatic vein, conveyed through the right side of the heart to the lungs, where it is probably consumed in the respiratory process, and thus contributes to the production of animal heat. The experiments of Lehmann led him to believe that the liver-sugar is converted into lactic acid previous to being finally disposed of in respiration.

The rapidity with which the sugar-forming process at the liver goes on seems to be influenced by various circumstances; but, on the whole, Bernard's experiments appear to prove that it is directly proportioned to the rapidity of the portal circulation. Whatever expedites this, increases the quantity formed, and *vice versâ*. Hence it is, probably, that irritation of various parts of the nervous system, especially of the sympathetic, causes an increased formation of sugar, by stimulating the portal circulation. The disease diabetes depends on an excessive activity of this function of the liver, though what originally occasions it still remains a mystery.

The majority of observers agree that the liver is the only organ engaged in the formation of sugar, except during intra-uterine life, when, as Bernard discovered, the placenta takes the part of the then inactive liver, and largely generates this important substance.*

* The whole subject of the sugar-forming process of the liver is still under examination. For a good analysis of Bernard's earlier obser-

### *Changes of the Food in the large Intestine.*

The uncertainty respecting the changes that the chyme undergoes in the small intestine has been already stated. Their general result is that the acid chyme is made alkaline, albumen again appears, the fatty and oily matters are reduced to a state of much more minute division, so that they make the fluid look almost creamy, various gases, chiefly carburets of hydrogen, are developed, and nearly all the nutritive materials of the food, as well as of the bile and other secretions discharged into the intestinal canal, are made capable of being absorbed by either the blood-vessels or the lacteals. The process of such absorption will be described hereafter: its result is that the mixture of chyme and the various secretions is gradually made more consistent and darker and, at the lower end of the small intestine, contains little more than the insoluble and indigestible matters, such as starch, woody fibre, horny matter, epithelium-cells, and mucus-corpuscles, epidermis of both vegetable and animal tissues, crystals of ammonio-magnesian phosphates and other salts, the colouring and fatty matters of the bile, and other excrementitious substances.

The contents of the small intestine continue to be alkaline until they pass into the cæcum, when they are said to become again acid. Different explanations have been given of this acidity, and of the purposes served by it. From the abundance and size of the tubular glands in the cæcum, it has been inferred that they secrete an acid fluid somewhat similar to the gastric juice, and capable of digesting those nutritive portions of food which have escaped the influence of the gastric secretion and

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vations see cxc. vol. xiii., 1854, p. 54, s. 3; and for a summary of nearly all that has been written lately on the subject, consult Valentin's and and Scherer's reports in Canstatt's Jahresberichte, and Dr. H. Weber's reports on Physiology, in the British and Foreign Medico-Chirurgical Review to 1860.

have passed unchanged through the small intestine. The fact that the cæcum is proportionably large in all Herbivora (except those that hybernate), supports the inference that it is an organ of special digestive properties, needed for a second or supplemental digestion of vegetable food. But respecting the acidity of the cæcum, Blondlot (xvi.) states, that in many herbivorous animals and granivorous birds, as sheep, goats, pigeons, and chickens, the contents of the cæcum were never acid, unless sugar in some form had been mixed with their food. He thinks that the acidity of the cæcum which then ensues is the result of that part of the starch or sugar which is not absorbed in the small intestine being transformed into lactic acid.

During the passage of the food, now becoming nearly all excrement, along the large intestine, fluid continues to be absorbed; and the mass gradually assumes the consistence and other characters of the fæces expelled from the intestinal canal by the combined action of the abdominal muscles and the muscular coat of the rectum.

The length of time required for the transit of food along the intestinal canal is dependent on many incidental circumstances. But an estimate of the average rate may be formed from the results of experiments by Tiedemann, who found that when he tied the common bile-duct of dogs, the excrements did not appear white until two days after the operation.

The average quantity of solid fæcal matter evacuated by the human adult in twenty-four hours is about five ounces. And if we take the diet-scale of the British navy as affording a fair estimate of the quantity of solid food consumed by an individual in the same time, viz., from 31 to 35½ ounces (lxxiv. p. 492), it will follow that from 26 to 30½ ounces of solid nutriment are absorbed into the system daily. The remaining five ounces consist almost entirely of insoluble and innutritious matter.

According to the analysis of Berzelius (xxiv. p. 268), which is adopted by Simon (lxxxii. vol. ii. p. 372) human fæces of

consistence sufficient to form a coherent mass are composed of—

| | | | |
|---|---|---|---|
| Water | | | 75·3 |
| Matters soluble in water | Bile | 0·9 | 5·7 |
| | Albumen | 0·9 | |
| | Peculiar extractive | 2·7 | |
| | Salts | 1·2 | |
| Insoluble residue of the food | | | 7·0 |
| Insoluble matters which are added in the intestinal canal,—mucus, biliary resin, fat, and a peculiar animal matter | | | 14·0 |
| | | | 102·0 |

The ashes of the human fæces have been analysed by Enderlin (x. 1844) who found that 100 parts yielded—

| | |
|---|---|
| Chloride of sodium and alkaline sulphate | 1·367 |
| Tribasic phosphate of soda | 2·633 |
| Phosphate of lime and phosphate of magnesia | 81·372 |
| Phosphate of iron | 2·091 |
| Sulphate of lime | 4·564 |
| Silica | 7·973 |
| | 100·000* |

*Movements of the Intestines.*

It remains only to consider the manner in which the food and the several secretions mingled with it are moved through the intestinal canal, so as to be slowly subjected to the influence of fresh portions of intestinal secretion, and as slowly exposed to the absorbent power of all the villi and blood-vessels of the mucous membrane. Their movement is *peristaltic* or *vermicular*, effected by the alternate contractions and dilatations of successive portions of the intestinal coats. The contractions, which may commence at any point of the intestine, extend in a wave-like manner along the tube. In any

* For the latest and most complete analysis of the excrements of man and Mammalia see a paper by Dr. Marcet in the Philosophical Transactions (1854. p. 265).

given portion, the longitudinal muscular fibres contract first, or more than the circular; they draw a portion of the intestine upwards, or, as it were, backwards, over the substance to be propelled, and then the circular fibres of the same portion contracting in succession from above downwards, or, as it were, from behind forwards, press on the substance into the portion next below, in which at once the same succession of actions next ensues. These movements take place slowly, and, in health, are commonly unperceived by the mind; but they are perceptible when they are accelerated under the influence of any irritant.

The movements of the intestines are sometimes retrograde; and there is no hindrance to the backward movement of the contents of the small intestine. But almost complete security is afforded against the passage of the contents of the large into the small intestine by the ileo-cæcal valve, an apparatus in which are combined the principles of construction observed in the valves of blood-vessels and in that of the pylorus. For it consists, essentially, of two wide semilunar folds of mucous membrane, which project from the end of the ileum into the cavity of the cæcum, and are so placed that when any of the contents of the cæcum are pressed back on them, they will first approximate their edges, and then press them together and hold them close, like the valves of veins. But besides, the orifice of communication between the ileum and cæcum (at the borders of which orifice are these folds of mucous membrane) is encircled with muscular fibres, the contraction of which prevents the undue dilatation of the orifice.

Proceeding from above downwards, the muscular fibres of the large intestine become, on the whole, stronger in direct proportion to the greater strength required for the onward-moving of the fæces, which are gradually becoming firmer. The greatest strength is in the rectum, at the termination of which a *sphincter* muscle is placed outside the longitudinal fibres, and holds the orifice close by a constant slight contraction under the influence of the spinal cord.

The peculiar condition of the sphincter, in relation to the nervous system, will be again referred to. The rest of the intestinal canal is under the direct influence of the sympathetic or ganglionic system, and, indirectly or more distantly, is subject to the influence of the brain and spinal cord, which influence appears to be, in some degree, transmitted through the vagus nerve. Experimental irritation of the brain or cord produces no evident or constant effect on the movements of the intestines during life; yet in consequence of certain conditions of the mind, the movements are accelerated or retarded, and in paraplegia the intestines appear, after a time, much weakened in their power, and costiveness and tympanitis ensue. After death, irritation of both the sympathetic and pneumogastric nerves, if not too strong, induces genuine peristaltic movements of the intestines. Violent or other irritation stops the movements, apparently, by exhausting the nervous influence, and thus paralysing the muscular tissue. These stimuli act no doubt, not directly on the muscular tissue of the intestine, but on the rich ganglionic structure shewn by Meissner (xxxiii. 2nd. Ser. vol. 8) to exist in the submucous tissue. This regulates and controls the movements and gives to them their peculiar slow, orderly, rhythmic, and peristaltic character, both naturally, and when artificially excited.*

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## CHAPTER IX.

### ABSORPTION.

THE process of absorption has, for one of its objects, the introduction into the blood of fresh materials from the food and air, and whatever comes into contact with the external or internal surfaces of the body; and, for another, the taking away

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* For late observations on this subject, see, especially, Professor Lister (cxxiii. Vol. ix. No. 32).

of parts of the body itself, when, having fulfilled their office, or otherwise requiring removal, they need to be renewed. In both these offices, *i. e.*, in both absorption from without and absorption from within, the process manifests some variety, and a very wide range of action; and in both it is probable that two sets of vessels are, or may be, concerned, namely, the blood-vessels, and the lacteals or lymphatics, to which the term absorbents has been especially applied.

The *lymphatics* are distributed in nearly all the parts of the body that contain blood-vessels, and convey a fluid termed *lymph;* the lacteals are confined exclusively to the intestinal canal, and, at certain times, contain the *chyle.* The difference between these two sets of vessels is more apparent than real; in structure they are nearly identical; they have a common trunk, the thoracic duct; and, for their contents, the chyle probably differs from the lymph only in that it contains, besides the lymph derived from the walls of the intestines as from other parts, certain elements of food absorbed through the intestinal villi, which give it a characteristic milky whiteness.

Absorption by the lacteals has been commonly described as *nutritive absorption*, because materials for nutrition are, by its means, conveyed into the blood; while absorption by the lymphatics has been more generally named *interstitial absorption*, and regarded merely as the means by which the several parts of the body are cleared of their waste and excrementitious materials, whether during growth or in common nutritive repair. But it is most probable that the latter purpose is effected by the absorption by blood-vessels; and that the lymphatics are in this again essentially similar to the lacteals, that they absorb and elaborate organizable principles, capable of being employed for further purposes in the economy.

### *Absorption by the Lacteal Vessels.*

During the passage of the chyme along the whole tract of the intestinal canal, its completely digested parts are absorbed

by the blood-vessels and lacteals distributed in the mucous membrane. The blood-vessels appear to absorb none but the dissolved portions of the food, and these, including especially the albuminous and saccharine, they imbibe without choice; whatever can mix with the blood passes into the vessels, as will be presently described. But the lacteals appear to absorb only certain constituents of the food, including particularly the fatty portions. The absorption by both sets of vessels is carried on most actively, but not exclusively, in the villi of the small intestine; for in these minute processes, both the capillary blood-vessels and the lacteals are brought almost into contact with the intestinal contents.

It has been already stated (p. 240) that the villi of the small intestine are minute vascular processes of mucous membrane, each containing a delicate network of blood-vessels, and one or more lacteals, which sometimes seem to ramify, and are usually invested by a sheath of cylindrical epithelium. In the interspaces of the mucous membrane between the villi, as well as over all the rest of the intestinal canal, the lacteals and blood-vessels are also densely distributed in a close network, (E. H. Weber, lxxx. 1847); the lacteals, however, being more sparingly supplied to the large than to the small intestine.

It has long been, and is still, very difficult to explain how absorption by the lacteals is effected. It was formerly supposed, that both the lacteals and the villi were perforated at their extremities, and that the absorption took place through the orifices: but there are no such orifices; the walls of the lacteals, like those of the blood-vessels, are everywhere complete and closed. From the fact that the blood-vessels in villi lie external to the lacteals, and hold nearly the same relation to them as in some secernent glands they do to the extremities of the gland-ducts, Valentin (iii. p. 142) was led to suggest that the chyle cannot be immediately transferred from the intestine to the lacteal vessels, but is absorbed first by the blood-vessels, and then, as it were, secreted

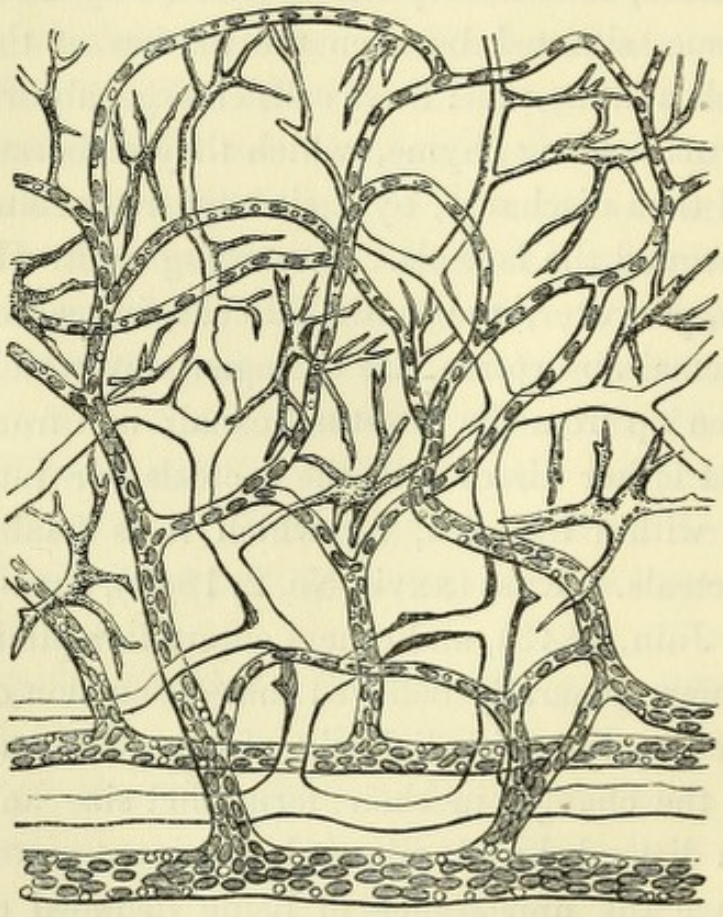
into the lacteals. More recent investigations, however, have made it nearly certain, that the abstraction of the elements of chyle from the intestine, and their transference into the lacteals, are effected through the instrumentality of cells, and that the blood in the blood-vessels of the villi is, probably, only so far subservient to the process, in that it may supply part of the nutritive material necessary to the growth of the cells. According to Goodsir (ii. p. 4), the cylindrical epithelium investing the villi is cast off at each period of digestion, so that the naked villi come into direct contact with the contents of the intestine, and absorption is effected by cells developed in the tissue, situated between the meshes of the capillary blood-vessels and the villi: these cells enlarge, absorb materials from the surrounding chyme, which they elaborate in their interior, and then discharge, by their rupture or solution, either into or around the lacteals. According to E. H. Weber (lxxx. 1847), however, the epithelial cells, instead of being shed during lacteal absorption, are the agents by which the chyle is first taken up from the intestinal canal; and from these it is transferred either direct into the lacteals, or into other cells situated within the villi, by which it is finally conveyed into the lacteals. Kuss (xxvii. No. 2, 1840), Gruby and Delafond (xviii, Juin, 1843), and others entertain a similar view : and it is now generally believed that absorption of chyle is really effected by the epithelial cells of the villi, and that it is owing to the change in their form and size and general aspect, when distended with oily and opalescent material, that the villi have the appearance of being denuded of epithelium. The fact that some of the cells contain an opaque-white, while others contain a transparent, oily fluid, supports the opinion that they possess the power of selecting and absorbing different materials That such selective power in lacteal absorption exists, is rendered further probable by the fact (which will be again referred to in connection with the absorption by blood-vessels), that when various odorous, colouring, and saline matters are introduced into the intestines, they pass

into the blood-vessels, but not into the lacteals; these, we may believe, being guarded from their entrance by the network of blood-vessels around them, and by the elaborating cells.

### *Absorption by the Lymphatics.*

The vessels for the absorption of lymph, are distributed in nearly all parts of the body. Their existence has not yet been determined in the main and spinal cord, the bones, cartilages, dense tendons, the eye, placenta, umbilical cord, membranes of the ovum, or any of the non-vascular parts, as the nails, cuticle, hair, and the like (xxv. 1842, p. 45). But it is probable that they exist in all the other parts that have blood-vessels.

*Fig.* 29.*



The lymphatics commence either in closely-meshed net-works, interspersed among the proper elements and blood-vessels of the several tissues, the size of the meshes and the width of the canals, varying like those of the capillary blood vessels (pl. 1, figs. 7 and 8): or else in pointed closed tubes or processes from the vessels, such as are shown in the

* Fig. 29. Capillary blood-vessels and lymphatics from the tail of the tadpole: showing the origin of the lymphatics from radiated cells, and by pointed processes. The blood-vessels are denoted by the corpuscles they contain.

annexed sketch of the lymph and blood-vessels in a part of the tail of the tadpole (fig. 29). In this state, many of the origins of the lymphatics communicate with pointed or star-shaped cells; but this may be peculiar to the embryonic state, for no similar cells are seen in the adult, neither is there any appearance of the existence of cells for the elaboration of lymph, similar to those described in the villi.

It has been supposed, that the lymphatics, at their origin and in the substance of absorbent glands, communicate directly with the blood-vessels; but there is not sufficient evidence for believing that this is ever the case in Mammalia and birds, although it may be so in Amphibia and fish (xxv. 1842, p. 45). In man and Mammalia, the lymphatics and blood-vessels are connected only by the principal lymphatic trunk, the thoracic duct, which opens into the juncture of the left internal jugular and subclavian veins, and by a corresponding but smaller trunk which pours its contents into the corresponding part on the right side.

The real nature of the substances absorbed by the lymphatic vessels, and the mode in which the absorption is effected, are still among the enigmas of physiology. It may, however, be held as highly probable, that the materials which it is the special object of the lymphatics to absorb, are, like those commonly absorbed by the lacteals, chiefly of a nutritive kind, capable of a higher organisation, and of contributing to the nutrition of the body. Whether these are derived exclusively from the liquor sanguinis effused for the nutrition of the tissues, or from the fluid with which the tissues are kept moist, or, in part also, from degenerated or used portions of the tissues, cannot yet with certainty be determined. Parts which, having entered into the composition of a tissue, and having fulfilled their purpose, require to be removed, may not be altogether excrementitious, but may admit of being re-organized and adapted to the nutrition of the same or some lower tissue; and these may be absorbed by the lymphatics. On the whole, however, it is most probable that the lymph is derived from

the liquor sanguinis; since changes in the character of the former usually correspond very closely with changes in the character of either the whole mass of blood, or of that in the vessels of the part from which the lymph is examined. Thus Herbst (cxxxiv.) found that the coagulability of the lymph is directly proportionate to that of the blood; and that when fluids are injected into the blood-vessels in sufficient quantity to distend them, the injected substance may be almost directly afterwards found in the lymphatics.

### *Properties of Chyle and Lymph.*

The fluid contained in the lacteals during fasting is clear and transparent, and differs in no respect from ordinary lymph; but, during absorption from the chyme, it becomes milky, and acquires the other characters of chyle.

The whiteness and opacity of chyle is due to the presence of innumerable particles of oily or fatty matter, of exceedingly minute, though nearly uniform size, measuring on the average about $\frac{1}{3000}$ of an inch (Gulliver, xxviii. p. 82, *note*). These constitute what Mr. Gulliver appropriately terms the *molecular base* of chyle. Their number, and consequently, the opacity of the chyle, are dependent upon the quantity of fatty matter contained in the food. Hence, as a rule, the chyle is whitest and most turbid in carnivorous animals; less so in Herbivora; while in birds it is usually transparent. The fatty nature of the molecules is made manifest by their solubility in ether, and, when the ether evaporates, by their being deposited in various-sized drops of oil.* Yet, since they do not run together and form a larger drop, as particles of oil would, it appears

* Some of the molecules may remain undissolved by the ether; but this appears to be due to their being defended from the action of the ether by being entangled within the albumen which it coagulates.

very probable that each molecule consists of oil coated over with albumen, in the manner in which, as Ascherson (lxxx. 1840) observed, oil always becomes covered when set free in minute drops in an albuminous solution. And this view is supported by the fact, that when water or dilute acetic acid is added to chyle, many of the molecules are lost sight of, and oil drops appear in their place, as if the investments of the molecules had been dissolved, and their oily contents had run together.

Except these molecules, the chyle taken from the villi or from lacteals near them, contains no other solid or organized bodies. The fluid in which the molecules float is albuminous, and does not spontaneously coagulate, though coagulable by the addition of ether. But as the chyle passes on towards the thoracic duct, and especially while it traverses one or more of the mesenteric glands (propelled by forces which will be described with the structure of the vessels), it is elaborated. The quantity of molecules and oily particles gradually diminishes; cells, to which the name of chyle-corpuscles is given, are developed in it; and by the development of fibrine, it acquires the property of coagulating spontaneously. The higher in the thoracic duct the chyle advances, the more is it, in all these respects, developed, the greater is the number of chyle-corpuscles, and the larger and firmer is the clot which forms in it when withdrawn and left at rest. Such a clot is like one of blood, without the red corpuscles; having the chyle-corpuscles entangled in it, and the fatty matter forming a white creamy film on the surface of the serum. But the clot of chyle is softer and moister than that of blood. Like blood, also, the chyle often remains for a long time in its vessels without coagulating, but coagulates rapidly on being removed from them (Bouisson, xix. 1844). The existence of fibrine in it is, therefore, certain; its increase appears to be commensurate with that of the corpuscles; and, like them, it is not absorbed as such from the chyme (for no fibrine exists in the chyle in the villi), but is gradually

elaborated out of the albumen which chyle, in its earliest condition, contains.

The structure of these chyle-corpuscles was described when speaking of the white or rudimentary corpuscles of the blood, with which they are identical (see pp. 48 and 65). Their mode of origin is obscure. It is possible that they are formed, as has been supposed, by an aggregation of some of the particles composing the molecular base of chyle; but such particles do not exist in lymph, in which, however, abundant corpuscles identical with those of chyle-corpuscles are found.

*Lymph*, under ordinary circumstances, is clear, transparent, and colourless, or of a pale yellow tint. It is devoid of smell, is slightly alkaline, like chyle, and has a saline taste. As seen with the microscope in the small transparent vessels of the tail of the tadpole, the lymph usually contains no corpuscles or particles of any kind; and it is probably only in the larger trunks in which, by a process similar to that described in the chyle, the lymph is more elaborated, that any corpuscles are formed. These corpuscles are already described; they are similar to those in the chyle, but less numerous. The fluid in which the corpucles float is commonly, and in health, albuminous, and contains no fatty particles or molecular base; but is liable to variations according to the general state of the blood, and that of the organ from which the lymph is derived. As it advances towards the thoracic duct, and passes through the lymphatic glands, it becomes, like chyle, spontaneously coagulable from the formation of fibrine.

From what has been said, it will appear that perfect chyle and lymph are, in essential characters, nearly similar, and scarcely differ, except in the preponderance of fatty matter in the chyle. The comparative analysis of the two fluids obtained from the lacteals and the lymphatics of a donkey, is thus given by Dr. Owen Rees (lxxi. Jan. 1841).

| | Chyle. | Lymph. |
|---|---|---|
| Water . . . . . | 90·237 | 96·536 |
| Albumen . . . . . | 3·516 | 1·200 |
| Fibrine . . . . . | 0·370 | 0·120 |
| Animal extractive . . . . | 1·565 | 1·559 |
| Fatty matter . . . . . | 3·601 | a trace. |
| Salts . . . . . | 0·711 | 0·585 |
| | 100·000 | 100·000 |

The analyses of Nasse afford an estimate of the relative compositions of the lymph, chyle, and blood, of the horse.*

| | Lymph. | Chyle. | Blood. |
|---|---|---|---|
| Water . . . . . | 950· | 935· | 810· |
| Corpuscles . . . | | 4· | 92·8 |
| Albumen . . . | 39·11 | 31· | 80· |
| Fibrine . . . | | 0·75 | 2·8 |
| Extractive matter . . | 4·88 | 6·25 | 5·2 |
| Fatty matter . . . | 0·09 | 15· | 1.55 |
| Alkaline salts . . . | 5·61 | 7· | 6·7 |
| Phosphate of lime and magnesia, oxyde of iron, etc. | 0·31 | 1· | 0·95 |
| | 1000· | 1000· | 1000· |

The contents of the thoracic duct, including both the lymph and chyle mixed, in an executed criminal, were examined by Dr. Rees, who found them to consist of 90·48 per cent. of water, 7·08 of albumen and fibrine, 0·108 of extractive, 0·92 of fatty, and 0·44 of saline matter.

From all these analyses of lymph and chyle, it appears that they contain essentially the same constituents as are found in the blood, viz., albumen, fibrine, and fatty matter, the same saline substances, and iron. Their composition differs from

* The analysis of the blood differs rather widely from that given at pages 50—51; but though it be erroneous, it is probable that corresponding errors exist in the analysis of the lymph and chyle; and that therefore the tables in the text may represent accurately enough the relation in which the three fluids stand to each other.

that of the blood in degree rather than in kind; they contain a less proportion of all the substances dissolved in the water (see Nasse's analyses, just quoted) and much less fibrine. The fibrine of lymph, besides being less in quantity, appears to be in a less elaborated state than that of the blood, coagulating less rapidly and less firmly. According to Virchow, it never coagulates, under ordinary circumstances, within the lymphatic vessels, either during life or after death (ccxxxiii. s. 143.) These differences gradually diminish, while the lymph and chyle, passing towards and through the thoracic duct, gradually approach the place at which they are to be mingled with the blood. For, in the thoracic duct, besides the higher and more abundant development of the fibrine, the lymph and chyle-corpuscles are found more advanced towards their development into red blood-corpuscles; sometimes even that development is completed, and the lymph has a pinkish tinge from the number of red blood-corpuscles that it contains.

The general result, therefore, of both the microscopic and the chemical examinations of the lymph and chyle, demonstrate that they are rudimental blood; their fluid part being like the liquor sanguinis diluted, but gradually becoming more concentrated; and their corpuscles being in process of development into red blood-corpuscles. Thus, in quality, the lymph and chyle are adapted to replenish the blood; and their quantity, so far as it can be estimated, appears ample. In one of Magendie's experiments, half an ounce of chyle was collected, in five minutes, from the thoracic duct of a middle-sized dog; Collard de Martigny obtained nine grains of lymph, in ten minutes, from the thoracic duct of a rabbit which had taken no food for twenty-four hours; and Geiger from three to five pounds of lymph daily from the foot of a horse, from whom the same quantity had been flowing several years without injury to the health. Bidder (lxxx. 1845) has found, on opening the thoracic duct in cats, immediately after death, that the mingled lymph and chyle continued to flow from one to

six minutes; and, from the quantity thus obtained, he estimated that if the contents of the thoracic duct continued to move at the same rate, the quantity which would pass into a cat's blood in twenty-four hours would be equal to about one-sixth of the weight of the whole body. And, since the estimated weight of the blood in cats is to the weight of their bodies as 1 : 1·7, the quantity of lymph daily traversing the thoracic duct would appear to be about equal to the quantity of blood at any time contained in the animals. By another series of experiments, Bidder estimated that the quantity of lymph traversing the thoracic duct of a dog in twenty-four hours, is about equal to two-thirds of the blood in the body. If we take these estimates, it will not follow from them that the whole of an animal's blood is daily replaced by the development of lymph and chyle; for even if the quantity of lymph and chyle daily formed be equal to that of the blood, the solid contents of the blood will be much too great to be replaced by those of the lymph and chyle. According to Nasse's analyses (p. 277), the solid matters of a given quantity of blood could not be replaced out of less than three or four times the quantity of lymph and chyle.

### *Office of the Lacteal and Lymphatic Vessels and Glands.*

The lacteal and lymphatic vessels serve not only to contain but to move the chyle and lymph. In structure, they are very like veins; having, according to Kölliker, an external coat of fibro-cellular tissue, with elastic filaments; within this, a thin layer of fibro-cellular tissue, with organic muscular fibres, which have, principally, a circular direction, and are much more abundant in the small than in the larger vessels; and, again, within this an inner elastic layer of longitudinal fibres, and a lining of epithelium; and numerous valves. The valves, constructed like those of veins, and with the free edges turned towards the heart, are usually arranged in pairs, and, in the small vessels, are so closely placed, that when the vessels are

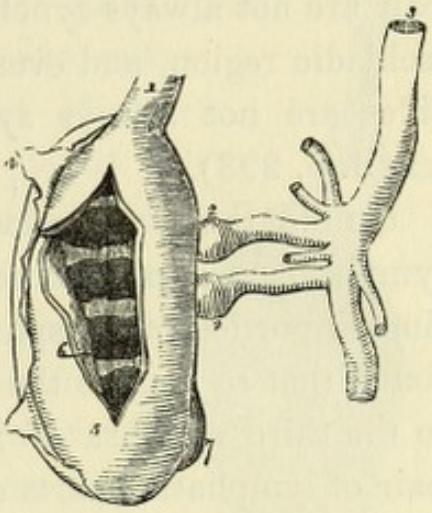
full, the valves constricting them where their edges are attached, give them a peculiar braided or knotted appearance (fig. 31, p. 283; and pl. 1, fig. 7).

With the help of the valvular mechanism, all occasional pressure on the exterior of the lymphatic and lacteal vessels propels the lymph towards the heart: thus muscular and other external pressure accelerates the flow of the lymph as it does that of the blood in the veins (see p. 132). The actions of the muscular fibres of the small intestines, and probably the layer of organic muscle present in each intestinal villus (p. 241), seem to assist in propelling the chyle: for, in the small intestine of a mouse, Poiseuille saw the chyle moving with intermittent propulsions that appeared to correspond with the peristaltic movements of the intestine. But for the general propulsion of the lymph and chyle, it is probable that, together with the *vis a tergo* resulting from absorption (as evidenced in the ascent of sap), and from external pressure, much of the force is derived from the contractility of the vessel's own walls. Kölliker, after watching the lymphatics in the transparent tail of the tadpole, states that no distinct movements of their walls can ever be seen, but as they are emptied after death they gradually contract, and then, after some time, again dilate to their former size, exactly as the small arteries do under the like circumstances (xxxi. 1846, p. 99). Thus, also, the larger vessels, in the human subject, commonly empty themselves after death; so that, although absorption is probably usually going on just before the time of death, it is not common to see the lymphatic or lacteal vessels full. Their power of contraction under the influence of stimuli has been demonstrated by Kölliker, who applied the wire of an electromagnetic apparatus to some well-filled lymphatics on the skin of a boy's foot, just after the removal of his leg by amputation, and noticed that the calibre of the vessels diminished at least one half (cxc. July, 1850). It is most probable that this contraction of the vessels occurs during life, and that it consists, not in peristaltic or undulatory movements, but in an uniform

contraction of the successive portions of the vessels, by which pressure is steadily exercised upon their contents, and which alternates with their relaxation.

In reptiles and some birds, an important auxiliary to the movement of the lymph and chyle is supplied in certain muscular sacs, named *lymph-hearts* (Fig. 30). The number and position of these organs vary. In frogs and toads there are usually four, two anterior and two posterior; in the frog the posterior lymph-heart on each side is situated in the ischiadic region just beneath the skin; the anterior lies deeper, just over the transverse process of the third vertebra. Into each of these cavities several lymphatics open: the orifices of the vessels being guarded by valves, which prevent the retrograde passage of the lymph. From each heart a single vein proceeds and conveys the lymph directly into the venous system. In the frog the inferior lymphatic heart, on each side, pours its lymph into a branch of the ischiadic vein; by the superior, the lymph is forced into a branch of the jugular vein, which issues from its anterior surface, and which becomes turgid each time that the sac contracts. Blood is prevented from passing from the vein into the lymphatic heart by a valve at its orifice.

*Fig.* 30.*



The muscular coat of these hearts is of variable thickness;

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* Fig. 30. Lymphatic heart (9 lines long, 4 lines broad), of a large species of serpent, the Python bivittatus, after E. Weber. 4. The external cellular coat. 5. The thick muscular coat. Four muscular columns run across its cavity, which communicates with three lymphatics (1—only one is here seen), with two veins (2, 2). 6. The smooth lining membrane of the cavity. 7. A small appendage, or auricle, the cavity of which is continuous with that of the rest of the organ.

in some cases it can only be discovered by means of the microscope; but in every case it is composed of transversely-striated fibres. The contractions of the hearts are rhythmical, occurring about sixty times in a minute, slowly, and, in comparison with those of the blood-hearts, feebly. The pulsations of the cervical pair are not always synchronous with those of the pair in the ischiadic region, and even the corresponding sacs of opposite sides are not always synchronous in their action (Müller, xxxii. p. 293).*

Unlike the contractions of the blood-heart, those of the lymph-heart appear to be directly dependent upon a certain limited portion of the spinal cord. For Volkmann (lxxx. 1844) found that so long as the portion of spinal cord corresponding to the third vertebra of the frog was uninjured, the cervical pair of lymphatic hearts continued pulsating, after all the rest of the spinal cord and the brain was destroyed; while destruction of this portion, even though all other parts of the nervous centres were uninjured, instantly arrested the heart's movements. The posterior or ischiadic pair of lymph-hearts were found to be governed, in like manner, by the portion of spinal cord corresponding to the eighth vertebra. Division of the posterior spinal roots did not arrest the movements; but division of the anterior roots caused them to cease at once.

*The Glands* placed on the lacteal and lymphatic vessels are something more than mere plexuses of the vessels.

Each gland has an investing capsule of connective tissue, from which prolongations dip into its substance forming partitions. Immediately within the investing capsule occurs what is named the cortical portion of the gland. It consists of a spongy alveolar tissue formed of septa of fibrous tissue, traversed by minute blood-vessels. The lacunæ or spaces in this tissue freely communicate with each other, and are filled

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* See also on the whole subject Stannius, lxxx. 1843; Panizza, lxxx. 1834, p. 300; E. Weber, lxxx. 1835, p. 535; and Valentin, xxxiv. Bd. i. p. 294.

with fluid containing nuclei and cells. They constitute, indeed, the direct continuations of the *afferent* lymphatic vessels which enter the gland, and after penetrating the capsule, lose their proper coats, and open out into these spaces in the cortical part of the gland. Afterwards they acquire fresh coverings, pass into the central or medullary part of the gland, where they form a dense plexus of vessels imbedded in a stroma of connective tissue; and then unite into one or more *efferent* vessels, which, on issuing from the gland, receive an external coat, and proceed on their way towards the thoracic duct (Fig. 31). No lymphatic or lacteal vessel joins the thoracic duct without thus passing through one or more glands. By the peculiar arrangement of the lymphatic vessels at the cortex of the glands, their contents are freely brought into relation in the lacunæ, with the capillary blood-vessels spread over the septa of these spaces, and a mutual interchange of materials and influence is thus allowed. The main result of this interchange appears to be the development of lymph-corpuscles, for it is well-known that the cell-contents of lymph and chyle beyond the glands is far greater than it was previously. An increase of fibrine also occurs as a consequence of the transit through the glands.

*Fig.* 31.*

### *Absorption by the Blood-vessels.*

The process thus named is that which has been commonly called *absorption by the veins;* but the term here employed

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* Fig. 31. A lymphatic gland from the axilla, with its afferent and efferent vessels, injected with mercury. After Bendz (lxxix.)

seems preferable, since, though the materials absorbed are commonly found in the veins, this is only because they are carried into them with the circulating blood, after being absorbed by all the blood-vessels (but chiefly by the capillaries) with which they were placed in contact. There is nothing in the mode of absorption by blood-vessels, or in the structure of veins, which can make them more active than arteries of the same size, or so active as the capillaries, in the process.

In the absorption by the lymphatics or lacteal vessels just described, there appears something like the exercise of choice in the materials admitted into them; for the chyle and lymph have a nearly constant composition, and we must admit, as an hypothesis, either that these vessels are so constructed that only certain materials, capable of being assimilated to their proper contents, can traverse the walls, or else that the materials from which the perfect chyle and lymph are to be developed are secreted into the lacteals and lymphatics from the adjacent blood-vessels. In either hypothesis, we assume something which brings the absorption by lacteals and lymphatics into the category of vital processes. But the absorption by blood-vessels presents no such appearance of selection of materials; rather, it appears, that every substance, whether gaseous, liquid, or a soluble or minutely-divided solid, may be absorbed by the blood-vessels, provided it is capable of permeating their walls, and of mixing with the blood; and that of all such substances, the mode and measure of absorption are determined solely by their physical or chemical properties and conditions, and by those of the blood and the walls of the blood-vessels.

While the question was being discussed, whether absorption (using the term generally) were effected by the lymphatics or the veins, many experiments were performed to demonstrate the fact of absorption by the blood-vessels, which may be quoted, not only as evidence for that fact, but in illustration of the difference between the absorption by lymphatics and

that by blood-vessels, in regard to the materials they severally receive and convey into the circulation.

Various odorous and saline matters taken with the food, or injected into the intestines of an animal, are soon found in the blood of the vena portæ, or other blood-vessels, or in the urine, but are not found in the chyle; or, if found there, not till they may have passed into the lacteals from their blood-vessels. This is shown by numerous experiments, especially by those of Tiedemann and Gmelin, and Panizza. The substances used in the experiments were ferrocyanate of potash, sulphate of potash, several salts of lead, iron, and other metals, indigo, madder, rhubarb, camphor, musk, alcohol, turpentine, etc. Mayer (xcvi. t. iii. p. 485) also, when he injected ferrocyanate of potash into the lungs, found it in the left side of the heart sooner than in the right; showing that it had taken the course of the blood, not of the lymph, which would have carried it to the right side of the heart first. All these substances, therefore, appear to be absorbed by blood-vessels exclusively.

Again, if any of these substances be included within a portion of an animal's intestine tied at both ends, and if all the vessels of that portion of the intestine be cut away, except its artery and vein, the substances being absorbed, will be found in the blood of the vein; but, if the main arteries and veins be tied, and the lacteals left entire, the same substances will not be found in them. So with poisons, such as opium and strychnia, in the experiments of Magendie (cxxxiii. p. 314) and Segalas (lxii. t. ii. p. 117). When one of these poisons was put into a piece of intestine, of which the lacteals were tied, but the blood-vessels were free, poisoning took place within six minutes after returning the intestine into the abdomen; but if the vein or veins of the piece of intestine were tied, so as to stop the circulation of blood, the effects of the poison were delayed for an hour or more, though the lacteals were free to absorb and carry it to the blood. The numerous experiments, proving that poisons are not absorbed, or only

very slowly, after insertion into the hinder extremities of animals in which the aorta or vena cava inferior is tied, tend to the same conclusion, that these are among the substances not absorbed by the lymphatic or lacteal vessels, but absorbed without choice by the blood-vessels.

It is, probably, a general truth, that in parts which are supplied with both blood-vessels and lymphatics, the lymphatics (or lacteals for the intestines) absorb only such materials as will form lymph and chyle for the replenishing of the blood, while the blood-vessels absorb all other materials, and such substances as are accidentally brought into contact with them. But in parts which receive only blood-vessels, such as the brain and spinal cord, the eye and placenta, and, probably, most of the bones, cartilages, and fibrous tissues, the blood-vessels alone must perform the whole function of absorption, as they do in the invertebrate animals.

The absorption by blood-vessels is the consequence of their walls being, like all other tissues of the body, porous and capable of imbibing fluids, and of the blood being so composed, that most fluids will mingle with it. The process of absorption, in an instructive, though very imperfect degree, may be observed in any portion of vascular tissue removed from the body. If such an one be placed in a vessel of water, it will shortly swell, and become heavier and moister, through the quantity of water imbibed or soaked into it; and if now, the blood contained in any of its vessels be let out, it will be found diluted with water, which has been absorbed by the blood-vessels and mingled with the blood. The water round the piece of tissue, also, will become blood-stained; and, if all be kept at perfect rest, the stain derived from the solution of the colouring matter of the blood (together with which chemistry would detect some of the albumen and other parts of the liquor sanguinis) will spread more widely every day. The same will happen if the piece of tissue be placed in a saline solution instead of water, or in a solution of colouring or odorous matter, either of which will give their tinge or

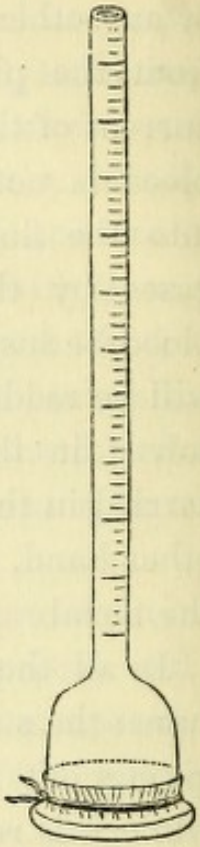
smell to the blood, and receive, in exchange, the colour of the blood.

Even so simple an experiment will illustrate the absorption by blood-vessels during life; the process, it shows, is imitated, but with these differences; that, during life, as soon as water or any other substance is admitted into the blood, it is carried from the place at which it was absorbed into the general current of the circulation; and that the colouring matter of the blood is not dissolved so as to ooze out of the blood-vessels into the fluid which they are absorbing. The absorption of gases by the blood may be simply imitated. If venous blood be suspended in a moist bladder in the air, its surface will be reddened by the contact of oxygen, which is first dissolved in the fluid that moistens the bladder, and is then carried in that fluid to the surface of the blood: while, on the other hand, watery vapour and carbonic acid will pass through the membrane, and be exhaled into the air.

In all these cases alike there is a mutual interchange between the substances; while the blood is receiving water, it is giving out its colouring matter and other constituents: or, while it is receiving oxygen, it is giving out carbonic acid and water; so that, at the end of the experiment, the two substances employed in it are mixed; and if, instead of a piece of tissue, one had taken a single blood-vessel full of blood, and placed it in water, both blood and water would, after a time, have been found both inside and outside the vessel. In such a case, moreover, if one were to determine accurately the quantity of water that passed to the blood, and that of blood that passed to the water, it would be found that the former was always greater than the latter. And so with other substances; it would almost always happen, that if the two fluids placed on opposite sides of a membrane were of different densities or specific gravities, a larger quantity of the less dense fluid would pass into the more dense, than of the latter into the former. M. Dutrochet, who made the earliest and best scientific investigation of this subject, having used in his experiments an appa-

ratus in which it was most convenient to allow the less dense fluid to pass into the more dense, employed the term *Endosmosis* to express the inward current, and *Exosmosis* for the outward one; and these terms, though they imply only the direction in which one or other of the two mixing fluids may happen to move in an experiment, are now used, the first, as the name of the more rapid, the second as that of the less rapid, stream. The instrument employed by M. Dutrochet was named an endosmometer (fig. 32). It may consist of a graduated tube expanded into a bell at one end, over which a portion of membrane may be tied. If now, the bell be filled with a fluid of much density, such as a strong solution of salt, and be immersed in one of less density, as water, the water will endosmose or pass into the solution, more rapidly than the solution will exosmose or pass out; but if the water were put in the bell and the saline solution outside, the directions of the currents would be reversed, and the names falsified; but the fact would remain the same, that the less dense would pass in a more rapid current than the more dense, till the two fluids were equally mixed on both sides of the membrane.

*Fig.* 32.



Although the instrument may have suggested inappropriate names, it is convenient both for experiment and to refer to in explanation of the process of the absorption of fluids by blood-vessels; for, as in the endosmometer we have a cavity filled with one fluid and separated by an organised membrane from another fluid, so, in the blood-vessels we have the blood separated by the organised walls of the vessels from whatever fluid or other substance may be placed in contact with their external surface; and the absorption by the blood-vessels is coarsely imitated by the fluid passing into the endosmometer more rapidly than that which it contains passes out.

Various opinions have been advanced in regard to the nature

of the force by which fluids of different densities and different chemical composition thus tend to mix through an intervening membrane. According to some, this power is solely physical and the result of the different degrees of capillary attraction exerted by the pores of the membrane upon the two fluids (see especially Power, cxliii. 1835, or an abstract of his paper in former editions of this Handbook): according to others, it is essentially chemical, one or other of the separated fluids decomposing and combining with the substance of which the membrane is composed, and thus passing through. Professor Graham has of late especially developed this latter view, which he believes to be remarkably adapted to explain the rapid interchange continually taking place between the fluids of living animal tissues. These fluids being usually either acid or alkaline, will naturally have a tendency to act chemically on the substance of an organic membrane or cell-wall, and thus to traverse them. He applies the term osmose, or osmotic force, to this chemical process, by which the mixture of fluids between intervening membranes is accomplished (xliii. 1854).*

Whatever view may be held as to the nature of the process, there are certain facts observed in experiments on the absorption by blood-vessels which may be here mentioned. With regard to the degree of absorption, much depends on the facility with which the substance to be absorbed can penetrate the membrane or tissue which lies between it and the blood-vessels; for, naturally, the blood-vessels are not bare to absorb. Thus absorption will hardly take place through the epidermis, but is quick when the epidermis is removed, and the same vessels are covered with only the surface of the cutis, or with granulations. In general, the absorption through membranes is in an inverse proportion to the thickness of their epithelia; so

* To gain an intelligible idea of Professor Graham's theory, it will be necessary for the student to consult the original essay, of which a satisfactory short abstract is scarcely possible.

Müller found the urinary bladder of a frog traversed in less than a second; and the absorption of poisons by the stomach or lungs appears sometimes accomplished in an immeasurably small time.

The substance to be absorbed must, as a general rule, be in the liquid or gaseous state, or if a solid, must be soluble in the fluids with which it is brought in contact. Hence, the marks of tattooing, and the discoloration produced by nitrate of silver taken internally remain. Mercury may be absorbed even in the metallic state; and in that state may pass into and remain in the blood-vessels, or be deposited from them (Oesterlen, viii. Feb. 1844); and such substances as exceedingly finely-divided charcoal, when taken into the alimentary canal, have been found in the mesenteric veins (Oesterlen, ix. 1847, p. 56); the insoluble materials of ointments may also be rubbed into the blood-vessels; but there are no facts to determine how these various substances effect their passage. Oil, minutely divided, as in an emulsion, will pass slowly into blood-veseels, as it will through a filter moistened with water (Vogel).

The less dense the fluid to be absorbed, the more speedy, as a general rule, is its absorption by the blood-vessels. Hence the rapid absorption of water from the stomach, and of weak saline solutions; but with strong solutions, there appears less absorption into, than effusion from, the blood-vessels.

The absorption is the less rapid the fuller and tenser the blood-vessels are, and the tension may be so great as to hinder altogether the entrance of more fluid. Thus, Magendie found that when he injected water into a dog's veins to repletion, poison was absorbed very slowly; but when he diminished the tension of the vessels by bleeding, the poison acted quickly. So, when cupping glasses are placed over a poisoned wound they retard the absorption of the poison, not only by diminishing the velocity of the circulation in the part, but by filling all its vessels too full to admit more. On the same ground, absorption is the quicker the more rapid the circulation of the

blood is; not because the fluid to be absorbed is more quickly imbibed into the tissues, or mingled with the blood, but because as fast as it enters the blood, it is carried away from the part, and the blood being constantly renewed, is constantly as fit as at the first for the reception of the substance to be absorbed.

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## CHAPTER X.

### NUTRITION AND GROWTH.

NUTRITION or nutritive assimilation is that modification of the formative process peculiar to living bodies (p. 28), by which tissues and organs already formed maintain their integrity. By the incorporation of fresh nutritive principles into their substance, the loss consequent on the waste and natural decay of the component particles of the tissues is repaired; and each elementary particle seems to have the power not only of attracting materials from the blood, but of causing them to assume its structure, and participate, in its vital properties. Thus, apparently from similar materials, nerves form nervous substance; muscles, muscular substance; and even morbid structures have the like assimilating power.

The differences between development, growth, and simple nutrition or maintenance, have been already stated (p. 29); under the head of NUTRITION will be now considered the process by which parts are maintained in the same general conditions of form, size, and composition, which they have already, by development and growth, attained; and this, notwithstanding, but rather by means of, continual changes in their

component particles. It is by this process, that an adult person, in health, is maintained, through a series of some years, with the same general outline of features, the same size and form, and perhaps even the same weight; although, during all this time, the several portions of his body are continually changing: their particles decaying and being removed, and then replaced by the formation of new ones, which, in their turn, also, die and pass away. Neither is it only a general similarity of the whole body which is thus maintained. Every organ and part of the body, as much as the whole, exactly maintains its form and composition, in the issue of the changes continually taking place among its particles.

The change of component particles, in which the nutrition of organs consists, is most evidently shewn when, in growth, they maintain their form and other general characters, but increase in size. When, for example, a long bone increases in circumference, and in the thickness of its walls, while, at the same time, its medullary cavity enlarges, it can only be by the addition of materials to its exterior, and a coincident removal of them from the interior of its wall; and so it must be with the growth of even the minutest portions of a tissue. And that a similar change of particles takes place, even while parts retain a perfect uniformity, may be proved, if it can be shewn that all the parts of the body are subject to waste and impairment.

In many parts, the removal of particles is evident. Thus, as will be shewn when speaking of secretion, the elementary structures composing glands are the parts of which the secretions are composed: each gland is constantly casting off its cells or their contents in the secretion which it forms: yet, each gland maintains its size and proper composition, because for every cell cast off a new one is produced. So also the epidermis and all such tissues are maintained. In the muscles, it seems nearly certain, that each act of contraction is accompanied with a change in the composition of the contracting tissue. Thence, the development of heat in acting muscles

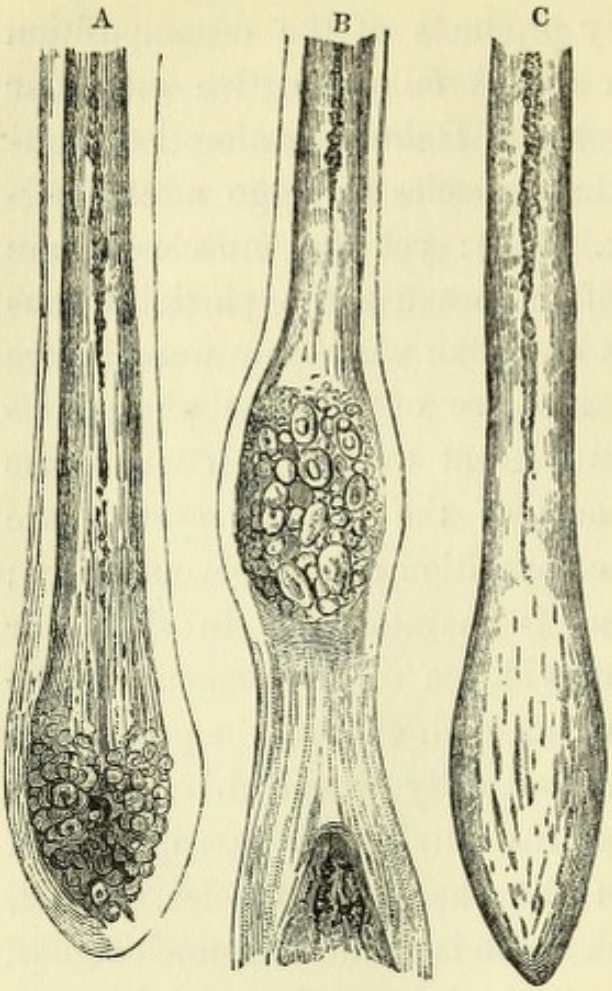
(p. 190), and thence, the increased discharge of urea, carbonic acid and water—the ordinary products of the decomposition of the animal tissues—which always follows active muscular exercise. Indeed, the researches of Helmholtz almost demonstrate the chemical change that muscles undergo after long-repeated contractions (lxxx. 1845): yet the muscles retain their structure and composition, because the particles thus changed are replaced by new ones like what they were before the change. So again, the increase of alkaline phosphates discharged with the urine after great mental exertion, seems to prove that the various acts of the nervous system are attended with change in the composition of the nervous tissue; yet the condition of that tissue is maintained. In short, for every tissue there is sufficient evidence of impairment in the discharge of its functions: without such change, the production or resistance of physical force is hardly conceivable: and the proof as well as the purpose of the nutritive process appears in the repair or replacement, of the changed particles, so that, notwithstanding its losses, each tissue is maintained unchanged.

But besides the impairment and change of composition to which all parts are subject in the discharge of their natural functions, an amount of impairment which will be in direct proportion to their activity, they are all liable to decay and degeneration of their particles, even while their natural actions are not called forth. It may be proved, as Dr. Carpenter first clearly shewed (cxxxi. p. 623), that every particle of the body is formed for a certain period of existence in the ordinary conditions of active life; at the end of which period, if not previously destroyed by outward force or exercise, it degenerates and is absorbed, or dies and is cast out.

The simplest examples that can be adduced of this are in the hair and teeth; and it may be observed, that, in the process which will now be described, all the great features of the process of nutrition seem to be represented.*

* These and other instances are related more in detail in the first six of Mr. Paget's Lectures on Surgical Pathology (ccix.) of which the

*Fig.* 33.*




An eyelash which naturally falls, or which can be drawn out without pain, is one that has lived its natural time, and has died, and been separated from the living parts. In its bulb such an one will be found different from those that are still living in any period of their age. In the early period of the growth of a dark eyelash, the medullary substance appears like an interior cylinder of darker granular substance, continued down to the deepest part, where the hair enlarges to form the bulb. This enlargement, which is of nearly cup-like form, appears to depend on the accumulation of nucleated cells, whose nuclei, according to their position, are, either by narrowing and elongation to form the fibrous substance of the outer part of the growing and further protruding hair, or are to be transformed into

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principal part of this chapter is an abstract. In connection with this subject, Mr. Paget's subsequent Lectures on Repair and Inflammation in the same work, may be consulted with advantage.

* Fig. 33. Intended to represent the changes undergone by a hair towards the close of its period of existence. At A its activity of growth is diminishing, as shewn by the small quantity of pigment contained in the cells of the pulp, and by the interrupted line of dark medullary substance. At B provision is being made for the formation of a new hair, by the growth of a new pulp connected with the pulp or capsule of the old hair. C. A hair at the end of its period of life, deprived of its sheath and of the mass of cells composing the pulp of a living hair.

the granular matter of its medullary portion. At the time of early and most active growth, all the cells and nuclei contain abundant pigment-matter, and the whole bulb looks nearly black. The sources of the material out of which the cells form themselves are, at least, two; the inner surface of the sheath, or capsule, which dips into the skin, enveloping the hair, and the surface of a vascular pulp which fits in a conical cavity in the bottom of the hair-bulb.

Such is the state of parts so long as the growing hair is all dark. But as the hair approaches the end of its existence, instead of the almost sudden enlargement at its bulb, it only swells a little, and then tapers nearly to a point: the conical cavity in its base is contracted; and the cells produced on the inner surface of the capsule contain no pigment. Still, for some time it continues thus to live and grow; and the vigour of the pulp lasts rather longer than that of the sheath or capsule, for it continues to produce pigment-matter for the medullary substance of the hair after the cortical substance has become white. Thus the column of dark medullary substance appears paler and more slender, and perhaps interrupted, down to the point of the conical pulp which, though smaller, is still distinct, because of the pigment-cells covering its surface.

At length the pulp can be no longer discerned, and uncoloured cells are alone produced, and maintain the latest growth of the hair. With these it appears to grow yet some further distance; for traces of the elongation of their nuclei into fibres appear in lines running from the inner surface of the capsule inwards and along the surface of the hair; and the column of dark medullary substance ceases at some distance above the lower end of the contracted hair-bulb. The end of all is the complete closure of the conical cavity in which the hair-pulp was lodged, the cessation of the production of new cells from the inner surface of the capsule, and the detachment of the hair which, as a dead part, is separated and falls.

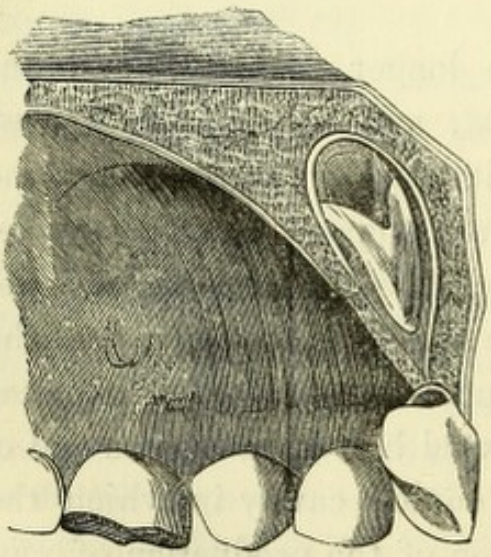
Such is the life of a hair, and such its death; which death

is spontaneous, independent of exercise, or of any mechanical external force — the natural termination of a certain period of life. Yet, before the hair dies, provision is made for its successor; for when its growth is failing, there appears below its base a dark spot, the germ or young pulp of the new hair covered with cells containing pigment, and often connected by a series of pigment cells with the old pulp or capsule (fig. 32, B).

Probably there is an intimate analogy between the process of successive life and death, and life communicated to a successor, which is here shewn, and that which constitutes the ordinary nutrition of a part. It may be objected, that the death and casting out of the hair cannot be imitated in internal parts; therefore, for an example in which the assumed absorption of the worn-out or degenerate internal particles is imitated in larger organs at the end of their appointed period of life, the instance of the deciduous or milk-teeth may be adduced.

Each milk-tooth is developed from its germ; and in the course of its own development, separates a portion of itself to be the germ of its successor; and each, having reached its perfection, retains for a time its perfect state, and still lives, though it does not grow. But at length, as the new tooth comes, the deciduous tooth dies; or rather, its crown dies, and is cast out like the dead hair, while its fang, with its bony sheathing, and vascular and nervous pulp, degenerates, and is absorbed (fig. 34). The degeneration is accompanied by some unknown spontaneous decomposition of the fang; for it

*Fig.* 34.*



* Fig. 34. Section of a portion of the upper jaw of a child, shewing a new tooth in process of formation, the fang of the corresponding deciduous tooth being absorbed.

could not be absorbed unless it was first so changed as to be soluble. And it is degeneration, not death, which precedes its removal; for when a toothfang dies, as that of the second tooth does in old age, then it is not absorbed, but is cast out entire, as a dead part.

Such, or generally such, it seems almost certain, is the process of maintenance by nutrition; the hair and teeth may be fairly taken as types of what occurs in other parts, for they are parts of complex organic structure and composition, and the teeth-pulps, which are absorbed as well as the fangs, are very vascular and sensitive.

Nor are they the only instances that might be adduced. The like development, persistence for a time in the perfect state, death, and discharge appear in all the varieties of cuticles and gland-cells; and in the epidermis, as in the teeth, there is evidence of decomposition of the old cells, in the fact of the different influence which acetic acid and potash exercise on them and on the younger cells. Seeing, then, that the process of nutrition, as thus displayed both in active organs and in elementary cells, appears, in these respects similar, the general conclusion may be that, in nutrition, the ordinary course of each complete elementary organ in the body, after the attainment of its perfect state by development and growth is, to remain in that state for a time; then, independently of the death or decay of the whole body, and in some measure, independently of its own exercise, or exposure to external violence, to die or to degenerate; and then, being cast out or absorbed, to make way for its successor.

It appears, moreover, that the length of life which each part is to enjoy is fixed and determinate, though, in some degree subject to accidents and to the expenditure of life in exercise. It is not likely that all parts are made to last a certain and equal time, and then all need to be changed. The bones, for instance, when once completely formed, must last longer than the muscles and other softer tissues. But, when we see that the life of certain parts is of determined length, whether they

be used or not, we may assume, from analogy, the same of nearly all.

Now, the deciduous human teeth have an appointed average duration of life. So have the deciduous teeth of all other animals; and in all the numerous instances of moulting, shedding of antlers, of desquamation, change of plumage in birds, and of hair in Mammalia, the only explanation is that these organs have their severally appointed times of living, at the ends of which they degenerate, die, are cast away, and in due time are replaced by others, which, in their turn, are to be developed to perfection, to live their life in the mature state, and in their turn, to be cast off. So also, in some elementary structures we may discern the same laws of determinate period of life, death, or degeneration, and replacement. They are evident in the history of the blood-corpuscles, both in the superseding of the first set of them by the second at a definite period in the life of the embryo, and in the replacement of those that degenerate by others new-formed from lymph-corpuscles (see pp. 62—70). And if we could suppose the blood-corpuscles grouped together in a tissue instead of floating, we might have in the changes they present an image of the nutrition of the elements of the tissues.

The *duration of life in each particle* is, however, liable to be modified; especially by the exercise of the function of the part. The less a part is exercised the longer do its component particles appear to live; the more active its functions are, the less prolonged is the existence of its individual particles. So in the case of single cells; if the general development of the tadpole be retarded by keeping it in a cold dark place, and if hereby the function of the blood-corpuscles be slowly and imperfectly discharged, they will maintain their embryonic state for even several weeks later than usual, the development of the second set of corpuscles will be proportionally postponed, and the individual life of the corpuscles of the first set will be, by the same time, prolonged.

Such being the modes in which the necessity for the process

of nutritive maintenance is created, such the sources of impairment and waste of the tissues, the next consideration may be, the manner in which the perfect state of a part is maintained by the insertion of new particles in the place of those that are absorbed or cast off.

The *process by which a new particle is formed* in the place of the old one is probably always a process of development; that is, the cell or fibre, or other element of tissue, passes in its formation, through the same stages of development as those elements of the same tissue did which were first formed in the embryo. This is probable from the analogy of the hair, the teeth, the epidermis, and all the tissues that can be observed: in all, the process of repair or replacement is effected through development of the new parts. The existence of nuclei or cytoblasts in nearly all parts that are the seats of active nutrition makes the same probable. For these nuclei, such as are seen so abundant in strong, active muscles, are not remnants of the embryonic tissue, but germs or organs of power for new formation, and their abundance often appears directly proportionate to the activity of growth. Thus, they are always abundant in the fœtal tissues, and those of the young animal; and they are peculiarly numerous in the muscles and the brain, and their disappearance from a part in which they usually exist is a sure accompaniment and sign of degeneration.

A difference may be drawn between what may be called *nutritive reproduction* and *nutritive repetition*. The former is shown in the case of the human teeth. As the deciduous tooth is being developed, a part of its productive capsule is detached, and serves as a germ for the formation of the second tooth; in which second tooth, therefore, the first may be said to be reproduced, in the same sense as that in which we speak of the organs by which new individuals are formed, as the reproductive organs. But in the shark's jaws, and others, in which we see row after row of teeth succeeding each other, the row behind is not formed of germs derived from the row

before: the front row is simply repeated in the second one, the second in the third, and so on. So, in cuticle, the deepest layer of epidermis-cells derives no germs from the layer above them; their development is not like a reproduction of the cells that have gone on towards the surface before them: it is only a repetition. So, as already pointed out, the blood is maintained by constant repetition of the process of the development of new corpuscles, new fibrine, and other materials from the lymph and chyle; the new corpuscles being not derived through germs separated from old ones. It is not improbable that much of the difference in the degree of repair, of which the several tissues are capable after injuries or diseases, may be connected with these differences in their ordinary mode of nutrition.

In order that the process of nutrition may be perfectly accomplished, certain conditions are necessary. Of these, the most important are: 1st. A right state and composition of the blood, from which the materials for nutrition are derived. 2. A regular and not far distant supply of such blood. 3. A certain influence of the nervous system. 4. A natural state of the part to be nourished.

1. This *right condition* of the blood does not necessarily imply its accordance with any known standard of composition, common to all kinds of healthy blood, but rather the existence of a certain adaptation between the blood and the tissues, and even the several portions of each tissue. Such an adaptation, peculiar to each individual, is determined in its first formation, and is maintained in the concurrent development and increase of both blood and tissues; and upon its maintenance in adult life, appears to depend the continuance of a healthy process of nutrition, or at least, the preservation of that exact sameness of the whole body and its parts, which constitute the perfection of nutrition. Some notice of the maintenance of this sameness in the blood has been given already (p. 69), in speaking of the power of assimilation which the blood exercises, a power exactly comparable with this of maintenance

by nutrition in the tissues. And evidence of the adaptation between the blood and the tissues, and of the exceeding fineness of the adjustment by which it is maintained, is afforded by the phenomena of symmetrical diseases, in which, in consequence of some morbid condition of the blood, a change of structure affects in an exactly similar way the precisely corresponding parts on the two sides of the body, and no other parts of even the same tissue.* These phenomena can only be explained on the assumption, 1st, of the complete and peculiar identity in composition in the corresponding parts of opposite sides of the body; and, 2ndly, of so precise and complete an adaptation between the blood and the several parts of each tissue, that a morbid material being present in the blood may destroy its fitness for the nutrition of one or two portions of any tissue, such as the skin or the bones, without affecting its fitness for the maintenance of other portions of the same tissue. But if the blood can be fit for the maintenance of one part, and unfit for the maintenance of another part of that which appears by every other test that we can apply, the very same tissue, how precise must that adaptation of the blood to the whole body be, by which in health, it is always capable of maintaining, not only the whole number of different organs and tisues, but all the different parts of every one of them.

2. The necessity of *an adequate supply of appropriate blood in or near the part to be nourished*, in order that its nutrition may be perfect, is shown in the frequent examples of atrophy of parts to which too little blood is sent, of mortification or arrested nutrition when the supply of blood is entirely cut off. and of defective nutrition when the blood is stagnant in a part. That the nutrition of a part may be perfect, it is also necessary that the blood should be brought sufficiently near to it

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* For examples and illustrations of symmetrical diseases, see two papers on the subject published by Dr. William Budd and Mr. Paget, in the twenty-fifth volume of the Medico-Chirurgical Transactions.

for the elements of the tissue to imbibe, through the walls of the blood-vessels, the nutritive materials which they require. The blood-vessels themselves take no share in the process of nutrition, except as carriers of the nutritive matter. Therefore, provided they come so near that this nutritive matter may pass by imbibition into the part to be nourished, it is comparatively immaterial whether they ramify within the substance of the tissue, or are distributed only on its surface or border.

The blood-vessels serve alike for the nutrition of the vascular and the non-vascular parts, the difference between which, in regard to nutrition, is less than it may seem (see p. 122). For the vascular, the nutritive fluid is carried in streams into the interior; for the non-vascular, it flows on the surface; but in both alike, the parts themselves imbibe the fluid; and though the passage through the walls of the blood-vessels may effect some change in the materials, yet all the process of formation is, in both alike, outside the vessels. Thus, in muscular tissue, the fibrils in the very centre of the fibre, nourish themselves; yet these are distant from all blood-vessels, and can only by imbibition receive their nutriment. So, in bones, the spaces between the blood-vessels are wider than in muscle; yet the parts in the meshes nourish themselves, imbibing materials from the nearest source. The non-vascular epidermis, though no vessels pass into its substance, yet imbibes nutritive matter from the vessels of the immediately subjacent cutis, and maintains itself, and grows. The instances of the cornea and vitreous humour are stronger, yet similar; and sometimes even the same tissue is in one case vascular, in the other not, as the osseous tissue, which, when it is in masses or thick layers, has blood-vessels running into it; but when it is in thin layers, as in the lachrymal and turbinated bones, has not. These bones subsist on the blood flowing in the minute vessels of the mucous membrane, from which the epithelium derives nutriment on one side, the bone on the other, and the tissue of the membrane itself on every side: a striking instance

how, out of the same materials, many tissues maintain themselves, each exercising its peculiar assimilative and self-formative power.

3. The third condition said to be essential to a healthy nutrition, is *a certain influence of the nervous system.*

It has been held that the nervous system cannot be essential to a healthy course of nutrition, because in plants and the early embryo, and in the lowest animals in which no nervous system is developed, nutrition goes on without it. But this is no proof that in animals which have a nervous system, nutrition may be independent of it; rather, it may be assumed, than in ascending development, as one system after another is added or increased, so the highest (and, highest of all, the nervous system) will always be inserted and blended in a more and more intimate relation with all the rest: according to the general law, that the interdependence of parts augments with their development.

The reasonableness of this assumption is proved by many facts shewing the influence of the nervous system on nutrition, and by the most striking of these facts being observed in the higher animals, and especially in man. The influence of the mind in the production, aggravation, and cure of organic diseases is matter of daily observation, and a sufficient proof of influence exercised on nutrition through the nervous system.

Independently of mental influence, injuries, either to portions of the nervous centres, or to individual nerves, are frequently followed by defective nutrition of the parts supplied by the injured nerves, or deriving their nervous influence from the damaged portions of the nervous centres. Thus, lesions of the spinal cord are sometimes followed by mortification of portions of the paralysed parts; and this may take place very quickly, as in a case by Sir B. C. Brodie (clvi. p. 309), in which the ankle sloughed within twenty-four hours after an injury of the spine. After such lesions also, the repair of injuries in the paralysed parts may take place less completely than in others; so, Mr. Travers mentions a case in

which paraplegia was produced by fracture of the lumbar vertebræ, and, in the same accident, the humerus and tibia were fractured. The former in due time united; the latter did not (xcviii. p. 436). The same fact was illustrated by some experiments of Dr. Baly, in which having, in salamanders, cut off the end of the tail, and then thrust a thin wire some distance up the spinal canal, so as to destroy the cord, he found that the end of the tail was reproduced more slowly than in other salamanders in whom the spinal cord was left uninjured above the point at which the tail was amputated (xxxii. p. 396). Illustrations of the same kind are furnished by the several cases in which division or destruction of the trunk of the trigeminal nerve has been followed by incomplete and morbid nutrition of the corresponding side of the face; ulceration of the cornea being not unfrequently one of the consequences of such imperfect nutrition.* Part of the wasting and slow degeneration of tissue in paralysed limbs is probably referable also to the withdrawal of nervous influence from them; though, perhaps, more is due to the want of use of the tissues.

Undue irritation of the trunks of nerves, as well as their division or destruction, is sometimes followed by defective or morbid nutrition. To this may be referred the cases in which ulceration of the parts supplied by the irritated nerves occurs frequently, and continues so long as the irritation lasts (see lxxi. vol. xxxix. p. 1022). Further evidence of the influence of the nervous system upon nutrition is furnished by those cases in which, from mental anguish, or in severe neuralgic headaches, the hair becomes grey very quickly, or even in a few hours. And to all these may, perhaps, be added the facts that where any particular nerves have been deficient, the parts corresponding to them have likewise always been absent; and

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* See the particulars of such a case by Mr. Stanley (lxxi. vol. 1, p. 531), and the cases by Mr. Dixon in the twenty-eighth volume of the Medico-Chirurgical Transactions; also the results of experiments on frogs by Stannius (lxxx. 1847, p. 458).

where any organ is wanting, there is generally a corresponding absence of the nerves. Tiedemann (xcix. vol. p. 76) relates three cases of absence of the olfactory nerves coincident with an imperforate state of the cribriform plate of the ethmoid bone and cleft palate. Absence of the eyes is also attended with absence of their nerves.

So many and various facts leave little doubt that the nervous system exercises an influence over nutrition as over other organic processes; and they cannot be explained by supposing that the changes in the nutritive processes are only due to the variations in the size of the blood-vessels supplying the affected parts.

The question remains, through what class of nerves is the influence exerted? When defective nutrition occurs in parts rendered inactive by injury of the motor nerve alone, as in the muscles and other tissues of a paralysed face or limb, it may appear as if the atrophy were the direct consequence of the loss of power in the motor nerves; but it is more probable that the atrophy is the consequence of the want of exercise of the parts; for if the muscles be exercised by artificial irritation of their nerves, their nutrition will be less defective (J. Reid). The defect of the nutritive process which ensues in the face and other parts, in consequence of destruction of the trigeminal nerve, must be referred more directly to the loss of influence exercised through sensitive or sympathetic nerves; for the motor nerves of the face and eye, as well as the olfactory and optic, have no share in the defective nutrition which follows injury of the trigeminal nerve; and one or all of them may be destroyed without any direct disturbance of the nutrition of the parts they severally supply.

The direct influence exercised by the sensitive and sympathetic nerves over the process of nutrition, thus proved in the case of the trigeminal nerve, is probably only an example of what is generally true. A similar influence is shewn in the cases in which sloughing of parts from injury or disease of the spinal cord has ensued earlier and more extensively when sen-

sation, than when motion alone was lost;* and in other cases in which the wasting of a paralysed limb is, after a certain time, more marked when both sensation and motion are impaired, than when the power of motion alone is interfered with.

It is not at present possible to say whether the influence on nutrition is exercised through the sensitive or through the sympathetic nerves which, in the parts on which the observation has been made, are generally combined in the same sheath. The truth perhaps is, that it may be exerted through either or both of these nerves. The defect of nutrition which ensues after lesion of the spinal cord alone, the sympathetic nerves being uninjured, and the general atrophy which sometimes occurs in consequence of diseases of the brain, seem to prove the influence of the cerebro-spinal system; while the observation of Magendie and Longet that destructive disease of the eye ensues more quickly after division of the trigeminal nerve in front of the Casserian ganglion, where it is joined by the sympathetic fibres which pass with it to the eye, than when the division is made between the ganglion and the brain, seems to prove the influence of the sympathetic more than of the sensitive nerves.

4. The fourth condition necessary to healthy nutrition is a healthy state of the part to be nourished. This seems proved by the very nature of the process, which consists in the formation of new parts like those already existing; for, unless the latter are healthy the former cannot be so. Whatever be the condition of a part, it is apt to be perpetuated by assimilating exactly to itself, and endowing with all its peculiarities, the new particles which it forms to replace those that degenerate. So long as a part is healthy, and the other conditions of healthy nutrition exist, it maintains its healthy condition. But, according to the same law, if the structure of a part be diseased

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* See a case of this kind, recorded by Mr. Curling, in the twentieth volume of the Medico-Chirurgical Transactions.

or in any way altered from its natural condition, the alteration is maintained; the altered, like the healthy structure is perpetuated. The same exactness of the assimilation of the new parts to the old, which is seen in the nutrition of the healthy tissues, may be observed also in those that are formed in disease. By it, the exact form and relative size of a cicatrix are preserved from year to year; by it, the thickening and induration to which inflammation gives rise are kept up, and the various morbid states of the blood in struma, syphilis, and other chronic diseases are maintained, notwithstanding all diversities of diet. By this precision of the assimilating process, may be explained the law that certain diseases occur only once in the same person, and that certain others are apt to recur frequently; because in both cases alike, the alteration produced by the first attack of the disease is maintained by the exact likeness which the new parts bear to the old ones.

The period, however, during which an alteration of structure may be exactly maintained by nutrition, is not unlimited; for in nearly all altered parts there appears to exist a tendency to recover the perfect state; and, in many cases, this state is, in time, attained. To this we may attribute the possibility of revaccination after the lapse of some years; the occasional recurrence of small-pox, scarlet-fever, and the like diseases, in the same person; the wearing out of scars, and the complete restoration of tissues that have been altered by injury or disease.

Such are some of the more important conditions which appear to be essential to healthy nutrition. Absence or defect of any one of them is liable to be followed by disarrangement of the process; and the various diseases resulting from defective nutrition appear to be due to the failure of these conditions, more often than to imperfection of the process itself.

## GROWTH.

Growth, as has been already observed (page 29), consists in the increase of a part in bulk and weight by the addition

to its substance of particles similar to its own, but more than sufficient to replace those which it loses by the waste or natural decay of its tissue. The structure and composition of the part remains the same; but the increase of healthy tissue which it receives is attended with the capability of discharging a larger amount of its ordinary function.

While development is in progress, growth and it, frequently go on together in the same part, as in the formation of the various organs and tissues of the embryo, in which, parts while they grow larger, are also gradually more developed until they attain their perfect state. But, commonly, growth continues after development is completed, and, in some parts, continues even after the full stature of the body is attained, and after nearly every portion of it has gained its perfect state in both size and composition.

Thus the heart, in healthy men, according to Dr. Clendinning's examinations (lxxi. vol. xxii. p. 450), ceases to grow only with the cessation of life. And, in certain conditions, this continuance, or a renewal, of growth may be observed in nearly every part of the body. When parts have attained the full size which in the ordinary process of growth they reach, and are then kept in a moderate exercise of their functions, they commonly (as already stated), retain almost exactly the same dimensions through the adult period of life. But when, from any cause, a part already full-grown in proportion to the rest of the body, is called upon to discharge an unusual amount of its ordinary function, the demand is met by a corresponding increase or growth of the part. Illustrations of this are afforded by the increased thickening of cuticle at parts where it is subjected to an unusual degree of occasional pressure or friction, as in the palms of the hands of persons employed in rough manual labour; by the enlargement and increased hardness of muscles that are largely exercised; and by many other facts of a like kind. The increased power of nutrition put forth in such growth is greater than might be supposed; for the immediate effect of increased exercise of a part must be a greater

using of its tissue, and might be expected to entail a permanent thinning or diminution of the substance of the part. But the energy with which fresh particles are formed is sufficient not only to replace completely those that are worn away, but to cause an increase in the substance of the part—the amount of this increase being proportioned to the more than usual degree in which its functions are exercised.

The growth of a part from undue exercise of its functions is always, in itself, a healthy process; and the increased size which results from it must be distinguished from the various kinds of enlargement to which the same part may be subject from disease. In the former case, the enlargement is due to an increased quantity of healthy tissue, providing more than the previous power to meet a particular emergency; the other may be the result of a deposit of morbid material within the natural structure of the part, diminishing, instead of augmenting, its fitness for its office. Such a healthy process of growth in a part attended with increased power and activity of its function may, however, occur as the consequence of disease in some other part; in which case it is commonly called *Hypertrophy*, *i.e.*, excess of nutrition. The most familiar examples of this are in the increased thickness and robustness of the muscular walls of the cavities of the heart in cases of continued obstruction to the circulation; and in the increased development of the muscular coat of the urinary bladder when, from any cause, the free discharge of urine from it is interfered with. In both these cases, though the origin of the growth is the consequence of disease, yet the growth itself is natural, and its end is the benefit of the economy; it is only common growth renewed or exercised in a part which had attained its size in due proportion to the rest of the body.

It may be further mentioned, in relation to the physiology of this subject, that when the increase of function, which is requisite in the cases from which hypertrophy results, cannot be efficiently discharged by mere increase of the ordinary tissue of the part, the development of a new and higher kind of tissue

is frequently combined with this growth. An example of this is furnished by the uterus, in the walls of which, when it becomes enlarged by pregnancy, or by the growth of fibrous tumours, organic muscular fibres, found in very small amount in its quiescent state, are then enormously developed, and provide for the expulsion of the fœtus or the foreign body. Other examples of the same kind are furnished by cases in which, from obstruction to the discharge of their contents, and a consequently increased necessity for propulsive power, the coats of reservoirs and of ducts become the seat of development of organic muscular fibres, which either did not exist in them before, or were present in very small quantity.

Respecting the mode and conditions of the process of growth, it needs only be said, that its mode seems to differ only in degree from that of common maintenance of a part; more particles are removed from, and many more added to a growing tissue, than to one which only maintains itself. But so far as can be ascertained, the mode of removal, the disposition of the removed parts, and the insertion of the new particles, are as in simple maintenance. The conditions also of growth are the same as those of common nutrition, and are equally or more necessary to its occurrence. When they are very favourable or in excess, growth may occur in the place of common nutrition. Thus hair may grow profusely in the neighbourhood of old ulcers, in consequence, apparently, of the excessive supply of blood to the hair-bulbs and pulps; bones may increase in length when disease brings much blood to them; cocks' spurs transplanted from their legs into their combs grow to an unnatural length; and, in the case of double organs, such as the kidneys, when one is destroyed, the other grows to a large size, apparently in consequence of the excess of urea which for a time exists in the blood, and which supplies one of the materials from which the contents of the kidney-cells are formed.

# CHAPTER XI.

## SECRETION.

SECRETION is the process by which materials are separated from the blood, and from the organs in which they are formed, for the purpose either of serving some ulterior office in the economy, or of being discharged from the body as excrement. In the former case, both the separated materials and the processes for their separation are termed *secretions;* in the latter, they are named *excretions.*

Most of the secretions consist of substances which, probably, do not pre-exist in the same form in the blood, but require special organs and a process of elaboration for their formation, *e. g.*, the liver for the formation of bile, the mammary gland for the formation of milk. The excretions, on the other hand, commonly or chiefly consist of substances which, as urea, carbonic acid, and probably uric acid, exist ready-formed in the blood, and are merely abstracted therefrom. If from any cause, such as extensive disease or extirpation of an excretory organ, the separation of an excretion is prevented, and an accumulation of it in the blood ensues, it frequently escapes through other organs, and may be detected in various fluids of the body. But this is never the case with secretions; at least with those that are most elaborated; for after the removal of the special organs by which any of them is elaborated, it is no longer formed. Cases sometimes occur, in which the secretion continues to be formed by the natural organ, but not being able to escape towards the exterior, on account of some obstruction, is re-absorbed into the blood, and afterwards discharged from it by exudation in other ways; but these are not instances of true vicarious secretion, and must not be thus regarded.

These circumstances, and their final destination are, however, the only particulars in which secretions and excretions can be distinguished; for in general, the structure of the parts engaged in eliminating excretions, *e.g.*, the kidneys, is as complex as that of the parts concerned in the formation of secretions. And since the differences of the two processes of separation, corresponding with those in the several purposes and destinations of the fluids, are not yet ascertained, it will be sufficient to speak, in general terms, of the process of separation or secretion.

Every secreting apparatus possesses, as essential parts of its structure, a simple and apparently textureless membrane, named the *primary* or *basement-membrane;* certain *cells;* and *blood-vessels*. These three structural elements are arranged together in various ways; but all the varieties may be classed under one or other of two principal divisions, namely, *membranes* and *glands*.

## SECRETING MEMBRANES.

The principal secreting membranes are the serous and synovial membranes, the mucous membranes, and the skin.*

The *serous membrane* are formed of fibro-cellular tissue, interwoven so as to constitute a membrane, the free surface of which is covered with a single layer of flattened cells, forming, in most instances, a simple *tesselated epithelium.* Between the epithelium and the subjacent layer of fibro-cellular tissue, is situated the primary or basement membrane (Bowman, lxxiii., art., *Mucous Membrane.* Goodsir, ii. p. 41).

In relation to the process of secretion, the layer of fibro-cellular tissues serves as a ground-work for the ramification of

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* The skin will be described in Chapter XIII.

blood-vessels, lymphatics, and nerves.* But it is absent in some instances, as in the arachnoid covering the dura mater, and in the interior of the ventricles of the brain. The primary membrane and epithelium are always present, and are concerned in the formation of the fluid by which the free surface of the membrane is moistened.

The serous membranes are of two principal kinds: 1st. Those which line visceral cavities, *e. g.*, the peritoneum, pericardium, pleuræ, arachnoid, and tunicæ vaginales. 2nd. The synovial membranes lining the joints, and the sheaths of tendons and ligaments, with which, also, are usually included the synovial bursæ, or *bursæ mucosæ*, whether these be subcutaneous, or situated beneath tendons that glide over bones.

The serous membranes form closed sacs, and exist wherever the free surfaces of viscera come into contact with each other, or lie in cavities unattached to surrounding parts. The viscera which are invested by a serous membrane, are, as it were, pressed into the shut sac which it forms, carrying before them a portion of the membrane, which serves as their investment. To the law that serous membranes form shut sacs, there is, in the human subject, one exception, viz.: the opening of the Fallopian tubes into the abdominal cavity,—an arrangement which exists in man and all Vertebrata, with the exception of a few fishes.

The principal purpose of the serous and synovial membranes is to furnish a smooth, moist surface, to facilitate the movements of the invested organ, and to prevent the injurious effects of friction. This purpose is especially manifested in joints, in which free and extensive movements take place; and in the stomach and intestines which, from the varying quantity and movements of their contents, are in almost constant motion upon one another and the walls of the abdomen.

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* For an account of the nerves of serous membranes, see Purkinje (lxxx. 1845); Bourgery (xix. Sept. 1845); Pappenheim (viii. Oct. 1845); and Rainey (xli. vol. xxix.)

The fluid secreted from the free surface of the serous membranes is, in health, rarely more than sufficient to ensure the maintenance of their moisture. The opposed surfaces of each serous sac, are at every point in contact with each other, and leave no space in which fluid can collect. After death, a larger quantity of fluid is usually found in each serous sac; but this, if not the product of manifest disease, is probably such as has transuded after death, or in the last hours of life, An excess of such fluid in any of the serous sacs, constitutes dropsy of the sac.

The fluid naturally secreted by the serous membranes appears to be identical, in general and chemical characters, with the serum of the blood, or with very dilute liquor sanguinis. It is of pale yellow or straw-colour, slightly viscid, alkaline, and, because of the presence of albumen, coagulable by heat. The presence of a minute quantity of fibrine, at least in the dropsical fluids effused into the serous cavities, is shown by their partial coagulation into a jelly-like mass, on the addition of fibrine or other animal substances, or on mixture with some other serous fluid (see p. 13 *note*). This similarity of the serous fluid to the liquid part of blood, and to the fluid with which most animal tissues are moistened, renders it probable that it is, in great measure, separated by simple transudation through the walls of the blood-vessels. The probability is increased by the fact that, in jaundice, the fluid in the serous sacs is, equally with the serum of the blood, coloured with the bile. But there is reason for supposing that the fluid of the cerebral ventricles and of the arachnoid sac are exceptions to this rule: for they differ from the fluids of the other serous sacs not only in being pellucid, colourless, and of much less specific gravity, but in that they seldom receive the tinge of bile in the blood, and are not coloured by madder, or other similar substances introduced abundantly into the blood.

It is also probable that the formation of synovial fluid is a process of more genuine and elaborate secretion, by means of

the epithelial cells on the surface of the membrane, and especially of those which are accumulated on the edges and processes of the synovial fringes (Goodsir, ii., Rainey, cxxiii. 1847); for, in its peculiar density, viscidity, and abundance of albumen, synovia differs alike from the serum of blood, and from the fluid of any of the serous cavities.

The *mucous membranes* line all those passages by which internal parts communicate with the exterior, and by which either matters are eliminated from the body or foreign substances taken into it. They are soft and velvety, and extremely vascular. Their basis, or proper texture, seems to belong to the albuminous structures. Their external surfaces are attached to various other tissues; in the tongue, for example, to muscle; on cartilaginous parts, to perichondrium; in the cells of the ethmoid bone in the frontal and sphenoid sinuses, as well as in the tympanum, to periosteum; in the intestinal canal, it is connected with a firm sub-mucous membrane, which on its exterior gives attachment to the fibres of the muscular coat. The internal, or free surface, of the mucous membranes is at every part invested with one or more layers of epithelial cells, which are separated from the vascular tissue by the layer of basement membrane.

The mucous membranes are described as lining certain principal tracts. 1. The *digestive tract* commences in the cavity of the mouth, from which prolongations pass into the ducts of the salivary glands. From the mouth it passes through the fauces, pharynx, and œsophagus, to the stomach, and is thence continued along the whole tract of the intestinal canal to the termination of the rectum, being in its course arranged in the various folds and depressions already described (chapter viii.), and prolonged into the ducts of the pancreas and liver, and into the gall-bladder. 2. The *respiratory tract* includes the mucous membrane lining the cavity of the nose, and the various sinuses communicating with it, the lachrymal canal and sac, the conjunctiva of the eye and eyelids, and the

prolongation which passes along the Eustachian tubes and lines the tympanum and the inner surface of the membrana tympani. Crossing the pharynx, and lining that part of it which is above the soft palate, the respiratory tract leads into the glottis, whence it is continued, through the larynx and trachea, to the bronchi and their divisions, which it lines as far as the branches of from $\frac{1}{30}$th to $\frac{1}{30}$th of an inch in diameter (Rainey, xli. vol. xxviii.). 3. The *genito-urinary* tract, which lines the whole of the urinary passages, from their external orifice to the termination of the tubuli uriniferi of the kidneys, extends into and through the organs of generation in both sexes, into the ducts of the glands connected with them, and in the female becomes continuous with the serous membrane of the abdomen at the fimbriæ of the Fallopian tubes.

Along each of the above tracts, and in different portions of each of them, the mucous membrane presents certain structural peculiarities adapted to the functions which each part has to discharge; yet in some essential characters mucous membrane is the same, from whatever part it is obtained. In all the principal and larger parts of the several tracts, it presents an external layer of epithelium, situated upon the *basement membrane*, and beneath this, a stratum of vascular tissue of variable thickness, which in different cases presents either out-growths in the form of papillæ and villi, or depressions or involutions in the form of glands. But, in the prolongations of the tracts, where they pass into gland-ducts and their finest branches, these constituents are reduced to the epithelium, the primary or basement-membrane, and the capillary blood-vessels spread over the outer surface of the latter in a single layer.

The primary, or basement-membrane, is a thin transparent layer, simple, homogeneous, and with no discernible structure, which on the larger mucous membranes that have a layer of vascular fibro-cellular tissue, may appear to be only the blastema or formative substance, out of which successive layers of

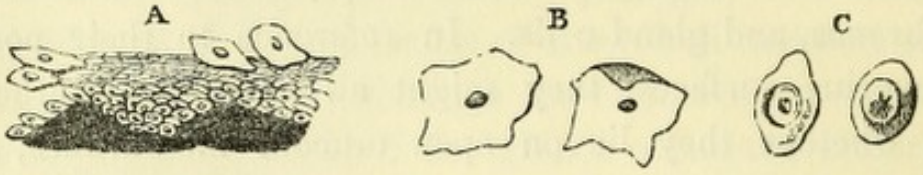
epithelium-cells are formed. But in the minuter divisions of the mucous membranes, and in the ducts of glands, it is the layer continuous and correspondent with this basement-membrane that forms the proper walls of the tubes. The cells also which, lining the larger and coarser mucous membranes, constitute their epithelium, are continuous with, and often similar to those which, lining the gland-ducts, are called *gland-cells*, rather than epithelium. Indeed, no certain distinction can be drawn between the epithelium-cells of mucous membranes, and gland-cells. In reference to their position, as covering surfaces, they might all be called epithelium-cells, whether they lie on open mucous membranes, or in gland-ducts; and in reference to the process of secretion, they might all be called gland-cells, or at least secreting-cells, since they probably all fulfil a secretory office by separating certain definite materials from the blood, and from the part on which they are seated. It is only an artificial distinction which makes them epithelial-cells in one place, and gland-cells in another.

It thus appears, that the tissues essential to the production of a secretion are, in their simplest form, a simple membrane, having on one surface blood-vessels, and on the other a layer of cells, which may be called either epithelium-cells, or gland-cells. The first two elements are so similar in all glands and mucous membranes, that it seems nearly certain that the cells are the principal agents in the process of secretion, a view which is confirmed by many other facts. It will therefore be explanatory of the whole process of secretion, if something be said now of the epithelia, or the secreting cells of the mucous membrane.

The *epithelia* present themselves under three different forms; the characters of each of which are different enough in well-marked examples, but when, as frequently happens, a continuous mucous surface possesses at different parts two or more different epithelia, there is a very gradual transition from one to the other.

The first and most common variety, as described by Henle (xxxvii. p. 220), is the *tesselated* or *pavement epithelium*, which is composed of flat, oval, roundish, or polygonal nucleated cells, of various size, arranged in one, or in many superposed layers (fig. 35). This form of epithelium is spread over the mouth, pharynx, and œsophagus, the conjunctiva covering the

*Fig.* 35.*




eye, the vagina, and entrance of the female urethra; a similar epithelium lines most of the serous and synovial membranes, also the blood and lymph-vessels; the outer covering of the skin, or epidermis (in the description of which a further account is given of this form of epithelium), is constructed on the same plan. Many gland-ducts also are lined with similar epithelium-cells; and the cells in the finest parts of these ducts, and in their extremities and most actively secreting parts, have a similar structure, though they are there usually spheroidal instead of flat.

The second variety is the *cylindrical* or *conical epithelium*, which extends from the cardiac orifice of the stomach along the whole of the digestive canal to the anus, and lines the various principal gland-ducts which open upon the mucous surface of this tract. It is also found in the greater part of the male genito-urinary apparatus, and the gland-ducts con-

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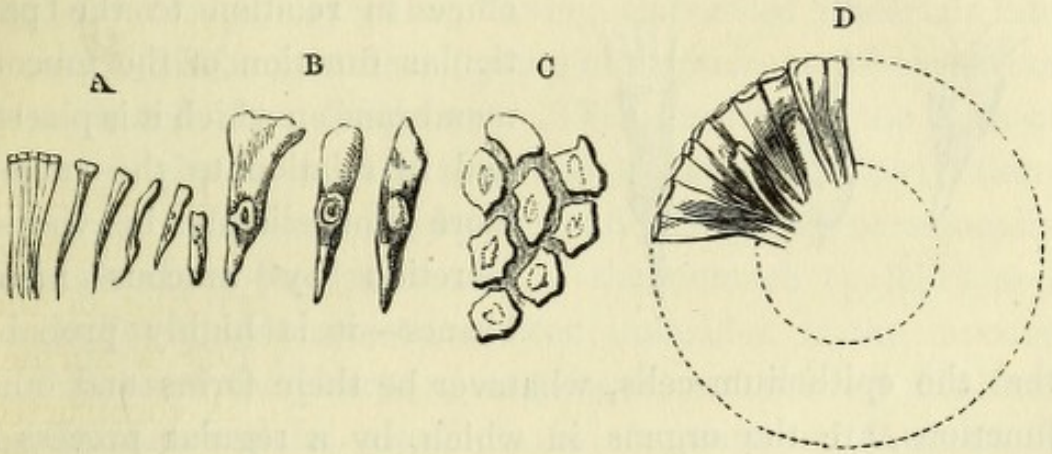
* Fig. 35. Scales of tesselated epithelium:—B. Scales taken from the inner surface of the cheek; the margin of one is folded, a frequent appearance of these scales, shewing their thinness and flexibility; C. the more deeply-seated or recently-formed scales or cellules from the human conjunctiva: A. section of the epithelium of the conjunctiva, with some scales loosened. After Henle.

nected with it; and lines the urinary passages of the female from the orifice of the urethra to the beginning of the urinary tubules of the kidneys. It is composed of closely-set cells of a conical, pyramidal, or cylindrical form, whose apices are attached to the mucous membrane or to flat epithelial cells lying upon it, and whose bases, which are usually terminated by a truncated plane, are free. Each of such cells encloses, at nearly mid-distance between its base and apex, a flat nucleus with nucleoli (fig. 36).

*Fig.* 36.*



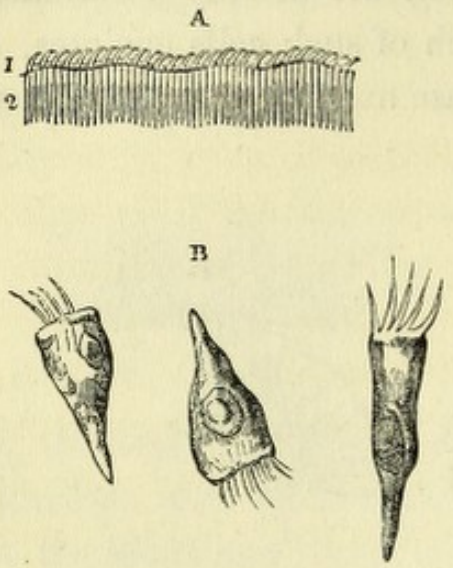

In the third variety of epithelium, cells, similar in other respects to the above, are provided at their free extremities with several fine pellucid pliant processes of cilia, which are constantly in rapid vibratory motion (fig. 37, p. 320). The nature of the movement of these cilia will be considered hereafter.† This form of epithelium lines the whole respiratory tract of mucous membrane and its prolongations. It occurs also in the female generative apparatus, commencing about the neck of the uterus, and extending to the fimbriated extremities of the Fallopian tubes, and for a short distance,

* Fig. 36. Cylinders of the intestinal epithelium, after Henle:—A. Cylinders from the cardiac region of the human stomach; B. the same from the jejunum; C. cylinders of the intestinal epithelium as seen when looking on their free extremities; D. ditto, as seen in a transverse section of a villus.

† See the chapter on MOTION.

along the peritoneal surface of the latter. A tesselated epithelium, with scales partly covered with cilia, lines the interior of the cerebral ventricles.

*Fig.* 37.*




These various kinds of epithelium serve one general purpose, namely, that of protecting and, at the same time, rendering smooth, the surfaces on which they are placed. But each also, probably, discharges a special office in relation to the particular function of the mucous membrane on which it is placed; and in relation to the subject more immediately in view—secretion by mucous membranes—it is highly probable that the epithelium-cells, whatever be their forms and other functions, are the organs in which, by a regular process of elaboration and secretion, such as will be presently described, the *mucus* of the several mucous membranes is formed and discharged. The general properties of mucus are already described (p. 15): the peculiarities characteristic of the mucus of each part are as yet imperfectly determined.

## SECRETING GLANDS.

The secreting glands are the organs to which the office of secreting is more especially ascribed: for they appear to be occupied with it alone. They all present, amid manifold diversities of form and composition, a general plan of structure, by which they are distinguished from all other textures of the

* Fig. 37. A. Cilia, as seen vibrating on a portion of the mucous membrane of the trachea of a rabbit; 1, the cilia; 2, lines indicating the several epithelial cells on which the cilia are placed. After Valentin. B. Separate cylinders of epithelium with cilia attached, from the trachea of the cat. After Henle.

body; especially, all contain, and appear constructed with particular regard to the arrangement of the cells, which, as already expressed, both line their tubes or cavities as an epithelium, and elaborate, as secreting cells, the substances to be discharged from them.

According to the different forms in which these cells are arranged, and the mode in which their contents are discharged, so are the several varieties of glands constructed and arranged in classes. In some, a single primary vesicle or sacculus, containing cells and nuclei, constitutes the whole gland; and such a sacculus, having elaborated materials into its cavity, discharges them by the absorption or dehiscence of its walls, and then disappears. This constitutes the class of *temporary* glands, or glands *without permanent orifices*: examples of which are furnished by the lenticular glands occasionally met with along the lesser arch of the stomach (p. 211), and the similar glands sometimes seen imbedded in the mucous membranes of the pharynx, œsophagus, and urinary bladder. The Graafian vesicles, also, both in structure and in mode of function, present many analogies to this form of glands.

These simple glands seem to serve only a temporary purpose, having discharged which they disappear, and are not reproduced until the occasion for them again rises. But in this fact lies their peculiar interest, in relation to the general physiology of secretion; since it is probable that their successive or periodical formation, the maturation of their contents, their discharge and temporary disappearance, represent very nearly the successive changes through which the acini or minutest lobules of the more complex glands pass.

These more complex glands, to which alone, till lately, the name of secreting glands was applied, may, for distinction as a class, be named *permanent glands*, or *glands with permanent ducts*. They comprise the great majority of glands; and for convenience of description may be further divided into three principal groups, the characters of each of which are deter-

mined by the different modes in which the sacculi or tubes containing the secreting cells are grouped.

1. The *simple tubule* or *tubular gland;* examples of which are furnished by the several tubular follicles in mucous membranes: especially by the follicles of Lieberkühn in the mucous membrane of the intestinal canal (p. 236), and the tubular or gastric glands of the stomach (p. 208). These appear to be simple tubular depressions of the mucous membrane on which they open, each consisting of an elongated gland-vesicle, the wall of which is formed of primary membrane, and is lined with secreting cells arranged as an epithelium. To the same class may be referred the elongated and tortuous sudoriparous glands of the skin, and the Meibomian follicles beneath the palpebral conjunctiva; though the latter are made more complex by the attachment of vesicles along their sides, and form a connecting link between the members of this division and the next, as the former by their length and tortuosity do between these and the third division.

2. The *aggregated glands*, including those that used to be called *conglomerate*, in which a number of vesicles or *acini* are arranged in groups or lobules. Such are all those commonly called mucous glands, as those of the trachea, vagina, and the minute salivary glands. Such, also, are the lachrymal, Brunnian, large salivary and mammary glands, Cowper's and Duverney's glands, the pancreas and prostate: the liver, also, has been by some included in this class, though the anatomy of its secreting structure is not yet satisfactorily determined. These various organs differ from each other only in secondary points of structure; such as, chiefly, the arrangement of their excretory ducts, the grouping of the *acini* and lobules, their connection by fibro-cellular tissue, and supply of blood-vessels. The acini commonly appear to be formed by a kind of fusion of the walls of several vesicles, which thus combine to form one cavity lined or filled with secreting cells, which also occupy recesses from the main cavity. The smallest branches of the gland-ducts sometimes open into the centres of these cavities;

sometimes the acini are clustered round the extremities, or by the sides, of the ducts: but, whatever secondary arrangement there may be, all have the same essential character of rounded groups of vesicles containing gland-cells, and opening, either occasionally or permanently, by a common central cavity into minute ducts, which ducts in the large glands converge and unite to form larger and larger branches, and at length, by one common trunk, open on a free surface of membrane (xxv. 1842, p. 48).

3. The *convoluted tubular glands*, such as the kidney and testis, form another division. These consist of tubules of membrane, lined with secreting cells arranged like an epithelium. Through nearly the whole of their long course, the tubules present an almost uniform size and structure; ultimately they terminate either in a cul-de-sac, or by dilating as in the Malpighian capsules of the kidney, or by forming a simple loop and returning as in the testicle.

Among these varieties of structure, all the permanent glands are alike in some essential points, besides those which they have in common with all truly secreting structures. They agree in presenting a large extent of secreting surface within a comparatively small solid space ; in the circumstance that while one end of the gland-duct opens on a free surface, the opposite end is always closed, having no direct communication with blood-vessels, or any other canals; and in an uniform arrangement of capillary blood-vessels, ramifying and forming a network around the walls and in their interstices of the ducts and acini.

## PROCESS OF SECRETION.

From what has been said, it will have already appeared that the modes in which secretions are produced are at least two. Some fluids, such as the secretions of serous membranes, appear to be simply exudations or oozings from the blood-vessels, whose qualities are determined by those of the liquor

sanguinis, while the quantities are liable to variation, or are chiefly dependent on the pressure of the blood on the interior of the blood-vessels. But, in the production of the other secretions, such as those of mucous membranes and all glands, other besides these mechanical forces are in operation. Most of the secretions are indeed liable to be modified by the circumstances which affect the simple exudation from the blood-vessels, and the products of such exudations, when excessive, are apt to be mixed with the more proper products of all the secreting organs. But the act of secretion in all glands is the result of the vital processes of cells or nuclei, which, as they develop themselves and grow, form in their interior the proper materials of the secretion, and then discharge them.

The best evidence for this view is: 1st. That cells and nuclei are constituents of all glands, however diverse their outer forms and other characters, and are in all glands placed on the surface or in the cavity whence the secretion is poured. 2nd. That many secretions which are visible with the microscope, may be seen in the cells of their glands before they are discharged. Thus, bile may be often discerned by its yellow tinge in the gland-cells of the liver; spermatozoids in the cells of the tubules of the testicles; granules of uric acid in those of the kidneys of fish, fatty particles like those of milk in the cells of the mammary gland.

The process of secretion might therefore be said to be accomplished in, and by the life of, these gland-cells. They appear, like the cells or other elements of any other organ, to develop themselves, grow, and attain their individual perfection by appropriating the nutriment from the adjacent blood-vessels and elaborating it into the materials of their walls and the contents of their cavities. In this perfected state, they subsist for some brief time, and when that period is over they appear to dissolve or burst and yield themselves and their contents as the peculiar material of the secretion. And this appears to be the case in every part of the gland that contains the appropriate gland-cells; therefore not in the extremities of

the ducts or in the acini alone, but in great part of their length.*

In these things there is the closest resemblance between secretion and nutrition; for, if the purpose which the secreting glands are to serve in the economy be disregarded, their formation might be considered as only the process of nutrition of organs, whose size and other conditions are maintained in, and by means of, the continual succession of cells developing themselves and passing away. In other words, glands are maintained by the development of the cells, and their continuance in the perfect state: and the secretions are discharged as the constituent gland-cells degenerate and are set free. The processes of nutrition and secretion are similar, also, in their obscurity: there is the same difficulty in saying why, out of apparently the same materials, the cells of one gland elaborate the components of bile, while those of another form the components of milk, and of a third those of saliva, as there is in determining why the cells of one tissue form cartilage, of another bone, of a third muscle, or any other tissue. In nutrition, also, as in secretion, some elements of tissues, such as the gelatinous tissues, are different in their chemical properties from any of the constituents ready-formed in the blood. Of these differences, also, no account can be rendered: but, obscure as the cause of these diversities may be, they are not objections to the explanation of secretion as a process similar to nutrition: an explanation with which all the facts of the case are reconcilable.

It may be observed that the diversities presented by the other constituents of glands afford no explanation of the differ-

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* Respecting the general anatomy of secreting glands, and the part performed by cells in the process of secretion, see, among others, Müller (cxlvii. and xxxii. p. 485); Simon (lxix. and xli. vol. xxx.); Bowman (lxxiii. art. *mucous membrane*); Carpenter (lxxiii. art. *Secretion*); Goodsir (ii.); and for a general account of the individual life of cells consult Carpenter (cxxxi.)

ences or peculiarities of their several products. There are many differences in the arrangements of the blood-vessels in different glands and mucous membranes; and, in accordance with these, much diversity in the rapidity with which the blood traverses them. But there is no reason for believing that these things do more than influence the rate of the process and the quantity of the material secreted. *Cæteris paribus*, the greater the vascularity of a secreting organ, and the larger the supply of blood traversing its vessels in a given time, the larger is the amount of secretion; but there is no evidence that the quantity or mode of movement of the blood can determine the quality of the secretion. The various modes and extents in which the basement-membrane is developed in different secreting organs have probably as little influence on the kind of secretion; for each of the several secretions is, in different animals, the product of glandular structures, widely various in their external form, and, on the other hand, very different fluids may be secreted by glands that, in the distribution of their ducts and vessels, are very similar (see especially Müller, xxxii.)

The *Discharge of Secretions* from glands may take place as soon as they are formed; or the secretion may be long retained within the gland or its ducts. The secretions of glands which are continually in active function for the purification of the blood, such as the kidneys, are generally discharged from the gland as rapidly as they are formed. But the secretions of those whose activity of function is only occasional, such as the testicle, are usually retained in the ducts during the periods of the gland's inaction. And there are glands which are like both these classes, such as the lachrymal and salivary, which constantly secrete small portions of fluid, and on occasions of greater excitement discharge it more abundantly. The modes, as well as the times in which secretions are discharged, are also various, or appear to be so. The glands that have not permanent ducts, discharge their mature contents by the rup-

ture or absorption of their cell-wall, and of the membrane over them; and, as already stated, it is not improbable that this represents a common mode of discharge, the secretions being first stored up in closed acini or vesicles at the ends, or by the sides, of the minutest ducts, and then opening into these by the absorption of their own walls, and of the adjacent portion of the basement membrane. But there is no sufficient proof of this; and the more general opinion seems to be, that the secreting cells are always enclosed within the ducts of the glands, or within cells or vesicles that always communicate with the ducts.

When discharged into the ducts, the further course of secretions is effected partly by the pressure from behind; the fresh quantities of secretion propelling those that were formed before. In the larger ducts, its propulsion is assisted by the contraction of their walls, All the larger ducts, such as the ureter and common bile-duct, possess in their coats organic muscular fibres; they contract when irritated, and sometimes manifest peristaltic movements (Müller xxxii. p. 521). Bernard and Brown-Séquard, indeed, have observed rhythmic contractions in the choledic and pancreatic ducts, and also in the ureters and vasa deferentia (ccxxviii. 1858), It is probable that the contractile power extends along the ducts to a considerable distance within the substance of the glands whose secretions can be rapidly expelled. Saliva and milk, for instance, are sometimes ejected with much force; doubtless, by the energetic and simultaneous contraction of many of the ducts of their respective glands. The contraction of the ducts can only expel the fluid they contain through their main trunk; for at their opposite ends all the ducts are closed. In disease, it is probable that the fibres of gland-ducts may be affected by a kind of spasm, or may be paralysed; either condition being succeeded by an impeded discharge of the secretion.

*Circumstances influencing Secretions.*—The influence of external conditions on the functions of glands, is manifested chiefly

in alterations of the quantity of secretion: and among the principal of these conditions are variations in the quantity of blood, in the quantity of the peculiar materials for any secretion that it may contain, and in the conditions of the nerves of the glands.

In general, an increase in the quantity of blood traversing a gland, coincides with an augmentation of its secretion. Thus, the mucous membrane of the stomach becomes florid when, on the introduction of food, its glands begin to secrete; the mammary gland becomes much more vascular during lactation; and it appears that all circumstances which give rise to an increase in the quantity of material secreted by an organ, produce, coincidently, an increased supply of blood. In most cases, the increased supply of blood rather follows than precedes the increase of secretion; as, in the nutritive processes, the increased nutrition of a part just precedes and determines the increased supply of blood; but, as also in the nutritive process, an increased supply of blood may have, for a consequence, an increased secretion from the glands to which it is sent.

Glands also secrete with increased activity, when the blood contains more than usual of the materials they are designed to separate. Thus, when an excess of urea is in the blood, whether from excessive exercise, or from destruction of one kidney, a healthy kidney will excrete more than it did before. It will, at the same time, grow larger; an interesting fact, as proving both that secretion and nutrition in glands are identical, and that the presence of certain materials in the blood may lead to the formation of structures in which they may be incorporated.

The production of secretions is, also, largely influenced by the condition of the nervous system. It is not possible to say, with certainty, whether the secretion of a gland would be arrested by the division or destruction of all the nerves distributed to it, for the branches of these nerves are largely spread over the blood-vessels, so that their destruction cannot be effected without serious injury to the vessels. Among the

best instances of nervous influence are those of secretion of the earthy phosphates, by the kidneys, after injury of the spinal cord. Whatever, within certain limits, excites the nerves of a gland, is followed by an increase in the quantity of its secretion. This is illustrated in the flow of tears and the increased discharge of saliva which often accompany a paroxysm of neuralgia in the fifth pair of nerves.

It appears immaterial to the perfection of secretion, from which nervous centres a secreting organ receives its supply of nervous influence; for some glands are supplied with sympathetic, others, with cerebro-spinal nerves, and others with both kinds; yet the mode of secretion appears to be in all alike. The experiments of Bernard (ccxvii.), Brown-Séquard (xxx. 1858), and others, however, seem to show that all secreting glands are provided with two distinct orders of nerves, namely motor and ganglionic: the latter appear to act by causing contraction of the blood-vessels supplying the gland, and thus diminishing the secretion, the former lead to dilatation of the vessels, and an abundant supply of blood, whereby the secretion is augmented. This was well shown in Bernard's experiments on the secretion of gastric fluid, irritation of the pneumogastric increasing it, irritation of the sympathetic branches of the semilunar ganglia diminishing or arresting it.

The exact mode, however, in which the nervous system influences secretion, must be still regarded as obscure. In many cases, it probably exerts its influence, as just said, by increasing or diminishing the quantity of blood supplied to the secreting gland, in virtue of the power which it exercises over the contractility of the smaller blood-vessels. Its influence over secretion, as well as over other functions of the body, may be excited by causes acting directly upon the nervous centres, upon the nerves going to the secreting organ, or upon the nerves of other parts. In the latter case, a reflex action is produced: thus, the impression produced upon the nervous centres by the contact of food in the mouth, is supposed to be

reflected upon the nerves supplying the salivary glands, and to produce, through these, a more abundant secretion of saliva.

Through the nerves, various conditions of the mind also influence the secretions. Thus, the thought of food may be sufficient to excite an abundant flow of saliva. And, probably, it is the mental state which excites the abundant secretion of urine in hysterical paroxysms, as well as the perspirations and occasional diarrhœa which ensue under the influence of terror, and the tears excited by sorrow or excess of joy. The quality of a secretion may also be affected by the mind; as in the cases in which, through grief or passion, the secretion of milk is altered, and is sometimes so changed, as to produce irritation in the alimentary canal of the child, or even death.*

The secretions of some of the glands seem to bear a certain relation or antagonism to each other, by which an increased activity of one is usually followed by diminished activity of one or more of the others; and a deranged condition of one is apt to entail a disordered state in the others. Such relations appear to exist among the various mucous membranes: and the close relation between the secretion of the kidney and that of the skin is a subject of constant observation.

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## CHAPTER XII.

### VASCULAR GLANDS: OR GLANDS WITHOUT DUCTS.

THE materials separated from the blood by the ordinary process of secretion by glands, are always discharged from the organ in which they are formed, and are either straightway expelled from the body, or if they are again received into the

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* See such cases by Carpenter (cxxxi. p. 476).

blood, it is only after they have been altered from their original condition, as in the cases of the saliva and bile. There appears, however, to be a modification of the process of secretion, in which certain materials are abstracted from the blood, undergo some change, and are added to the lymph or restored to the blood, without being previously discharged from the secreting organ, or made use of for any secondary purpose. The bodies in which this modified form of secretion takes place, are usually described as vascular glands, or glands without ducts, and include the spleen, the thymus and thyroid glands, the supra-renal capsules, the tonsils, and, according to Œsterlen and Ecker, and Gull, the pineal gland and pituitary body.

Peyer's glands of the intestine, and absorbent glands in general, also closely resemble them; indeed, both in structure and function, the vascular glands bear a close relation, on the one hand to the true secreting glands, and on the other to the lymphatic glands.

The evidence in favour of the view that these organs exercise a function analogous to that of secreting glands, has been chiefly obtained from recent investigations into their structure, which have shewn that all the glands without ducts contain the same essential structures as the secreting glands, except the ducts. They are mainly composed of vesicles, or sacculi, either simple and closed, as in the thyroid (Simon lxix.), spleen, and supra-renal capsules (Ecker lxx.), or variously branched, and with the cavities of the several branches communicating in and by common canals, as in the thymus (Simon lxix.*). These vesicles, like the acini of secreting

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* For all relating to the minute structure and functions of the vascular glands, consult the important works of the two above-mentioned authors, and of Œsterlen (cli.), Kölliker (lxxiii. art. *Spleen*, ccxii. and ccxviii.), Gray (ccxiii.), Wharton Jones (cxc. vol. xi. p. 32), Huxley (ccxvii. 1854), Sanders (clxxxix. 1852), Friedleben (ccxxxiv.), Julius Evans (xxx. 1844), Harley, on the supra-renal capsules (xxx. June, 1858; and Brown-Séquard (ccxxviii.). For the rough anatomy consult

glands, are formed of a delicate homogeneous membrane, are surrounded with and often traversed by a vascular plexus, and are filled with finely molecular albuminous fluid, suspended in which are either granules of fat, or cytoblasts or nuclei, or nucleated cells, or a mixture of all these.

These general resemblances in structure between the vascular glands and the true secernent glands lead to the supposition that both sets of organs pursue, up to a certain point, a similar course in the discharge of their functions. It is assumed that certain principles in an inferior state of organization are effused from the vessels into the sacculi, and gradually develope themselves into nuclei or cytoblasts, which may be further developed into cells; that in the growth of these nuclei and cells, the materials derived from the blood are elaborated into a higher condition of organization; and that, when liberated by the dissolution of the cells, they pass into the lymphatics, or are again received into the blood, whose aptness for nutrition they contribute to maintain.

The opinion that the vascular glands thus serve for the higher organization of the blood, is supported by their being all especially active in the discharge of their functions during fœtal life and childhood, when, for the development and growth of the body, the most abundant supply of highly-organized blood is necessary. The bulk of the thymus gland, in proportion to that of the body appears to bear almost a direct proportion to the activity of the body's development and growth, and when, at the period of puberty, the development of the body may be said to be complete, the gland wastes, and finally disappears. The thyroid gland and supra-renal capsules, also, though they probably never cease to discharge some amount of function, yet are proportionally much smaller in childhood than in fœtal life and infancy; and with the years

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Müller (xxxii. p. 615); and, for what relates to the fluids contained in the several glands, see, in addition to the works already quoted, Gulliver (xxviii). Ecker's work on the supra-renal capsules is translated into the London Medical Gazette, May, 1848; and for an abstract of Œsterlen's observations, see xxv. 1844-5, p. 28.

advancing to the adult period, they diminish yet more in proportionate size and apparent activity of function. The spleen more nearly retains its proportionate size, and enlarges nearly as the whole body does.

The function of the vascular glands seems not essential to life, at least not in the adult. The thymus wastes and disappears; no signs of illness attend some of the diseases which wholly destroy the structure of the thyroid gland; and the spleen has been often removed in animals, and in a few instances in men, without any evident ill-consequence. It is possible that, in such cases, some compensation for the loss of one of the organs may be afforded by an increased activity of function in those that remain. The experiment, to be complete, should include the removal of all these organs, an operation hardly possible without immediate danger to life. Nor, indeed, would this be certainly sufficient, since there is reason to suppose that the duties of the spleen, after its removal, might be performed by lymphatic or lacteal glands, between whose structure and that of the vascular glands there is much resemblance, and which, it is said, have been found peculiarly enlarged when the spleen has been removed (Mayer, lxxviii. March, 1845).

Although the functions of all the vascular glands may be similar, in so far as they may all alike serve for the elaboration and maintenance of the blood, yet each of them probably discharges a peculiar office, in relation either to the whole economy, or to that of some other organ. Respecting the special office of the thyroid gland, nothing reasonable can be suggested; nor is there any certain evidence concerning that of the supra-renal capsules.* Respecting the thymus gland,

* Mr. J. Hutchinson, following out Dr. Addison's discovery, has, by the collection of a large and valuable series of cases in which the supra-renal capsules were diseased, demonstrated most satisfactorily the very close relation subsisting between disease of these organs and brown discoloration of the skin; but the explanation of this relation is still involved in obscurity, and consequently does not aid much in determining the function of the supra-renal capsules (see cciv. 1856).

the observations of Mr. Simon (lxix.), confirmed by those of Friedleben (ccxxxiv.) and others, have shewn that in the hybernating animals, in which it exists throughout life, as each successive period of hybernation approaches, the thymus greatly enlarges and becomes laden with fat, which accumulates in it and in fat-glands connected with it, in even larger proportions than it does in the ordinary seats of adipose tissue. Hence it appears to serve for the storing up of materials which, being re-absorbed in the inactivity of the hybernating period, may maintain the respiration and the temperature of the body in the reduced state to which they fall during that time.

With respect to the office of the spleen, recent investigations seem to have furnished us with more definite information. In the first place, the large size which it gradually acquires towards the termination of the digestive process, and the great increase observed about this period in the amount of the finely-granular albuminous plasma within its parenchyma, and the subsequent gradual decrease of this material, seem to indicate that this organ is concerned in elaborating the albuminous or formative materials of food, and for a time storing them up, to be gradually introduced into the blood, according to the demands of the general system. The small amount of fatty matter in such plasma leads to the inference that the gland has little to do in regard to the preparation of material for the respiratory process.

Then, again, it seems not improbable that, as Hewson originally suggested, the spleen, and perhaps, to some extent, the other vascular glands, are, like the lymphatic glands, engaged in the formation of the germs of subsequent blood-corpuscles. For it seems quite certain, that the blood of the splenic vein contains an unusually large amount of white corpuscles: and in the disease termed leucocythæmia, in which the pale corpuscles of the blood are remarkably increased in number, there is almost always found an hypertrophied state of the spleen or thyroid body, or some of the lymphatic glands. Accordingly there seems to be a close analogy in function be-

tween the so-called vascular and the lymphatic glands: the former elaborating albuminous principles, and forming the germs of new blood-corpuscles out of alimentary materials absorbed by the blood-vessels; the latter discharging the like office on nutritive materials taken up by the general absorbent system. In Kölliker's opinion, the development of colourless and also coloured corpuscles of the blood is one of the essential functions of the spleen, into the veins of which the new-formed corpuscles pass, and are thus conveyed into the general current of the circulation (cxviii. 1860, p. 374.)

There is reason to believe too, that at the spleen many of the red-corpuscles of the blood, those probably which have discharged their office and are worn out, undergo disintegration; for in the coloured portion of the spleen-pulp an abundance of such corpuscles, in various stages of degeneration, are found, while the red-corpuscles in the splenic venous blood are said to be relatively diminished. According to Kölliker's description of this process of disintegration, the blood-corpuscles, becoming smaller and darker, collect together in roundish heaps, which may remain in this condition, or become each surrounded by a cell-wall. The cells thus produced may contain from one to twenty blood-corpuscles in their interior. These corpuscles become smaller and smaller; exchange their red for a golden-yellow, brown, or black colour; and, at length, are converted into figment-granules, which by degrees become paler and paler, until all colour is lost. The corpuscles undergo these changes whether the heaps of them are enveloped by a cell-wall or not (ccxviii. 1860, p. 365.)

Besides these, its supposed direct offices, the spleen is believed to fulfil some purpose, in regard to the portal circulation, with which it is in close connection. From the readiness with which it admits of being distended, and from the fact that it is generally small while gastric digestion is going on, and enlarges when that act is concluded, it is supposed to act as a kind of vascular reservoir, or diverticulum to the portal sys-

tem, or more particularly to the vessels of the stomach. That it may serve such a purpose is also made probable by the enlargement which it undergoes in certain affections of the heart and liver, attended with obstruction to the passage of blood through the latter organ, and by its diminution when the congestion of the portal system is relieved by discharges from the bowels, or by the effusion of blood into the stomach. This mechanical influence on the circulation, however, can hardly be supposed to be more than a very subordinate part of the office of an organ of so great complexity as the spleen, and containing so many other structures besides blood-vessels. The same may also be said, with regard to the opinion that the thyroid gland is important as a diverticulum for the cerebral circulation, or the thymus for the pulmonary in childhood. These, like the spleen, must have peculiar and higher, though as yet ill-understood, offices.

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## CHAPTER XIII.

### THE SKIN AND ITS SECRETION.

To complete the consideration of the processes of organic life, and especially of those which, by separating materials from the blood, maintain it in the state necessary for the nutrition of the body, a part of the physiology of the skin must be now considered: for besides the several purposes which it serves, as an external integument for the protection of the deeper tissues, and as a sensitive organ in the exercise of tact or touch, it is also an important excretory and absorbing organ; and of all its functions, that of excretion is the most directly necessary to the maintenance of life. Its office

as a sensitive integument will be considered in the chapter on Touch: here, it will be regarded chiefly in relation to its functions of excretion and absorption.

### *Structure of the Skin.*

The skin consists, principally, of a peculiar layer of vascular tissue, named the *corium, derma* or *cutis vera*, and an external covering of epithelium termed the *cuticle* or *epidermis*. Within and beneath the corium are imbedded several organs with special functions, namely, sudoriparous glands, hair-follicles, and sebaceous glands; and on its surface are sensitive papillæ.

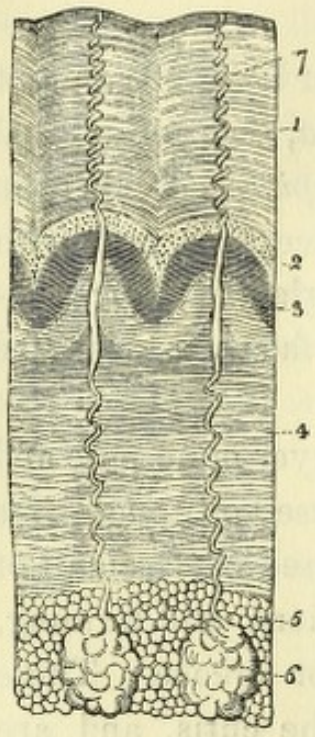
The *corium* or *cutis*, which rests upon a layer of adipose and cellular tissue of varying thickness, is a dense and tough, but yielding and highly elastic structure, composed of fasciculi of fibro-cellular tissue, interwoven in all directions, and forming, by their interlacements, numerous spaces or areolæ. These areolæ are large in the deeper layers of the cutis, and are there usually filled with little masses of fat: but, in the more superficial parts they are exceedingly small or entirely obliterated.

The *papillæ* are minute conical or cylindriform elevations, which are more prominent and more densely set at some parts, as the palmar surface of the hands and fingers, than at others. On these parts, and on the plantar surface of the feet and toes, they are disposed in double rows, in parallel curved lines, separated from each other by depressions. Thus they may be seen easily on the palm, whereon each raised line is composed of a double row of papillæ, and is intersected by short transverse lines or furrows corresponding with the interspaces between the successive pairs of the papillæ. (For structure and functions of the papillæ see Sense of Touch.)

In the middle of each of these transverse furrows, and irregularly scattered between the bases of the papillæ in other parts of the surface of the body, are the orifices of ducts of the

*sudoriparous glands,* by which it is probable that a large portion of the aqueous and gaseous materials excreted by the skin are separated. Each of these glands consists of a small lobular mass, which appears formed of a coil of tubular gland-duct, surrounded by blood-vessels and embedded in the subcutaneous adipose tissue (fig. 38). From this mass, the duct ascends, for a short distance, in a spiral manner through the deeper part of the cutis, then passing straight, and then sometimes again becoming spiral, it passes through the cuticle and opens by an oblique valve-like aperture. In the parts where the epidermis is thin, the ducts themselves are thinner and more nearly straight in their course (fig. 39). The canal of the duct, which maintains nearly the same diameter throughout, is lined with a layer of epithelium continuous with the epidermis; and its walls are formed of pellucid membrane continuous with the surface of the cutis.

*Fig.* 38.*




The sudoriparous glands are abundantly distributed over the whole surface of the body; but are especially numerous, as well as very large, in the skin of the palm of the hand where, according to Krause, they amount to 2736 in each superficial square inch (xv. article *Haut*), and according toMr. Erasmus Wilson to as many as 3528 (xxxv.). They are almost equally abundant and large in the skin of the sole. The glands by which the peculiar odorous matter of the axillæ is secreted form a nearly complete layer under the cutis, and are like the ordinary sudoriparous glands, except in being larger and

* Fig. 39. A perpendicular section of the skin of the palm of the hand, after Gurlt, shewing:—1. The epidermis; 2. The rete mucosum; 3. The papillæ; 4. The cutis; 5. The subcutaneous adipose tissue; 6. The sudoriparous glands; and 7. Their ducts.

having very short ducts (Robin, xix. Sept. 1845; Horner, xxxvi. Jan. 1846). In the neck and back, where they are least numerous, the glands amount to 417 on the square inch (Krause). Their total number Krause estimates at 2,381,248; and, supposing the orifice of each gland to present a surface of $\frac{1}{56}$th of a line in diameter (and regarding a line as equal to $\frac{1}{10}$th of an inch), he reckons that the whole of the glands would present an evaporating surface of about eight square inches.

*Fig.* 39.*

Besides the perspiration, the skin secretes a peculiar fatty matter, and for this purpose is provided with another set of special organs, termed *sebaceous glands* (fig. 39), which, like the sudoriparous glands, are abundantly distributed over most parts of the body. They are most numerous in parts largely supplied with hair, as the scalp and face, and are thickly distributed about the entrances of the various passages into the body, as the anus, nose, lips, and external ear. They are entirely absent from the palmar surfaces of the hands and the plantar surfaces of the feet. They are minutely lobulated glands, which appear composed of an aggregate of small vesicles or sacculi filled with opaque white substance, like soft ointment.† Minute capillary vessels overspread them; and their ducts, which have a beaded ap-

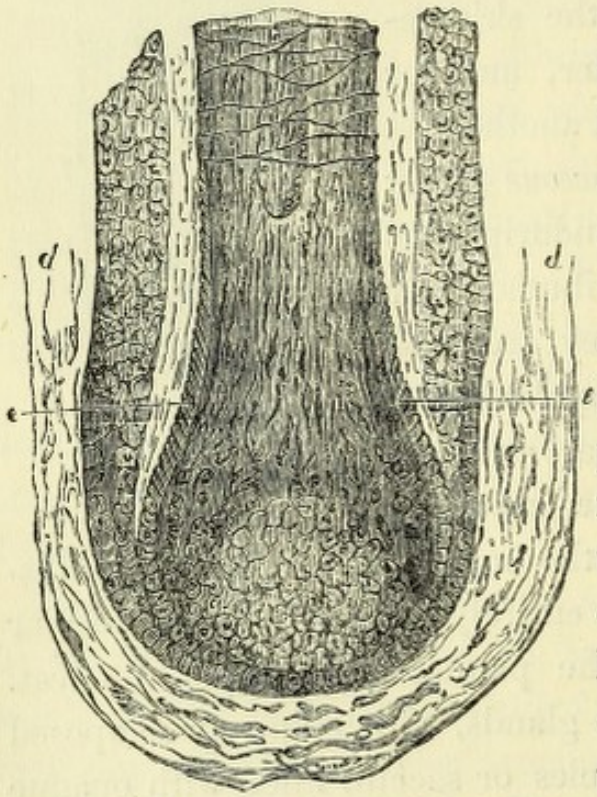
* Fig. 39. Sebaceous and sudoriparous glands of the skin, after Gurlt:—1. The thin cuticle; 2. The cutis; 3. Adipose tissue; 4. A hair, in its follicle (5); 6. Sebaceous gland, opening into the follicle of the hair by an efferent duct; 7. The sudoriparous gland.

† The peculiar bitter yellow substance secreted by the skin of the external auditory passage is named *cerumen*, and the glands themselves *ceruminous* glands; but they do not differ in structure from the other sebaceous glands.

pearance, as if formed of rows of cells, open either on the surface of the skin close to a hair, or, which is more usual, directly into the follicle of the hair. In the latter case, there are generally two glands to each hair (fig. 39). The ducts of these glands are very commonly tenanted by one or more entozoa, of a species named Acarus folliculorum. (Erasmus Wilson, xliii. 1844, p. 305; Gruby, xviii., March, 1845).

The *hair-follicles*, into which the sebaceous glands open, may also be reckoned among the secreting organs of the skin, since it is only at their lowest part that the material produced from their walls is appropriated to the growth of hair. The follicles are tubular depressions from the surface of the skin, descending into the subcutaneous fat, generally to a greater depth than the sudoriparous glands, and at their deepest part enlarging in a bulbous form, and often curving from their previous rectilinear course (fig. 40). They are lined throughout with cells of epithelium, continuous with those of the epidermis, and their walls are formed of pellucid membrane, which, commonly, in the follicles of the largest hairs, has the structure of vascular fibro-cellular tissue. The cells lining the deepest part of the follicles contribute to the growth of the hair; those in the rest of their extent, though like epithelial cells in their

*Fig.* 40.*




* Fig. 40. Root of a hair and its follicle, magnified 200 times. *a.* stem or shaft of the hair cut transversely; *b.* the inner, and *e.* the outer layer of the epidermic lining of the follicle; *d.* the dermic or external coat of the follicle; *c.* imbricated scales about to form a cortical layer on the surface of the hair (after Kohlrausch.)

arrangement, are doubtless gland-cells in function, and secrete a part of the material by which the hairs and the surface of the skin are anointed.*

Such are the glands of the skin: but it is with it, as with the glands in general; together with the formed secretions, fluids pass through it by mere oozing from the blood-vessels, and gases and watery vapour are exhaled from its free surface. This evaporation, however, is much limited by the *epidermis*, which is composed of layers of tesselated or pavement-epithelium cells. Its cells are flattened, oval, or polygonal, and average about $\frac{1}{1900}$th of an inch in diameter; each contains a nucleus, which again contains one or more distinct, and several paler granules. The thickness of the epidermis on different portions of the skin is directly proportioned to the friction, pressure, and other sources of injury to which it is exposed, and the more it is subjected to such injury, within certain limits, the more does it grow, and the thicker and more horny does it become; for it serves as well to protect the sensitive and vascular cutis from injury from without, as to limit the evaporation of fluid from the blood-vessels. The adaptation of the epidermis to the latter purposes may be well shewn by exposing to the air two dead hands or feet, of which one has its epidermis perfect, and the other is deprived of it: in a day, the skin of the latter will become brown, dry, and horn-like, while that of the former will almost retain its natural moisture.

### *Excretion by the Skin.*

The skin, as already stated, is the seat of a two-fold excretion: of that formed by the sebaceous glands and hair-follicles,

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* On the Structure of the Skin and its Glands, see Breschet (xlv.); Henle (xxxvii.); E. Wilson (xliv.); Todd and Bowman (xxxix.); Kölliker (ccvi., ccxii., and ccxviii., 1860); Huxley (lxxiii. Art. *Tegumentary Organs*); and other works on General Anatomy.

and of the more watery fluid, the sweat or perspiration, eliminated by the sudoriparous glands.

The secretion of the sebaceous glands and hair follicles (for their products cannot be separated) consists of cast-off epithelium cells, with nuclei and granules, together with an oily matter, extractive matter, and stearine; in certain parts, also, it is mixed with a peculiar odorous principle. It is, perhaps, nearly similar in composition to the unctuous coating, or vernix caseosa, which is formed on the body of the fœtus while in the uterus, and which contains large quantities both of oleine and margarine (J. Davy, xli. vol. xxvii. p. 189). Its purpose seems to be that of keeping the skin moist and supple, and, by its oily nature, of both hindering the evaporation from the surface, and guarding the skin from the effects of the long-continued action of moisture. But while it thus serves local purposes, its removal from the body entitles it to be reckoned among the excretions of the skin; though the share it has in the purifying of the blood cannot be discerned.

The fluid secreted by the sudoriparous glands is usually formed so gradually, that the watery portions of it escape by evaporation as fast as it reaches the surface. But, during strong exercise, exposure to great external warmth, in some diseases, and when evaporation is prevented by the application of oiled silk or plaister, the secretion becomes more sensible and collects on the skin in the form of drops of fluid. A good analysis of the secretion of these glands, unmixed with other fluids secreted from the skin, can scarcely be made; for the quantity that can be collected pure is very small. Krause (lv.) in a few drops from the palm of the hand, found an acid reaction, oily matter, and margarine, with water.

The perspiration of the skin, as the term is commonly employed in physiology, includes all that portion of the secretions and exudations from the skin that is capable of evaporation; the sweat includes all that may be collected in drops of fluid on the surface of the skin. The former is also often called insensible perspiration: the latter, sensible perspiration.

The fluids are the same, except that the sweat is commonly mingled with various substances lying on the surface of the skin. The contents of the sweat are, in part, matters capable of assuming the form of vapour, such as carbonic acid and water, and in part, other matters which are deposited on the skin, and mixed with the sebaceous secretion. Thenard collected the perspiration in a flannel shirt which had been washed in distilled water, and found in it chloride of sodium, acetic acid, some phosphate of soda, traces of phosphate of lime, and oxide of iron, together with an animal substance. In sweat which had run from the forehead in drops, Berzelius found lactic acid, chloride of sodium, and muriate of ammonia (xxiv). Anselmino placed his arm in a glass cylinder, and closed the opening around it with oiled silk, taking care that the arm touched the glass at no point. The cutaneous exhalation collected on the interior of the glass, and ran down as a fluid: on analysing this, he found water, acetate of ammonia, and carbonic acid; and in the ashes of the dried residue of sweat he found carbonate, sulphate, and phosphate of soda, and some potash, with chloride of sodium, phosphate and carbonate of lime, and traces of oxide of iron. Urea has also been shown to be an ordinary constituent of the fluid of perspiration (ccxxi. p. 301). Of these several substances, none, however, need particular consideration, except the carbonic acid and water.

The quantity of watery vapour excreted from the skin, was estimated very carefully by Lavoisier and Seguin. The latter chemist enclosed his body in an air-tight bag, with a mouth-piece. The bag being closed by a strong band above, and the mouth-piece adjusted and gummed to the skin around the mouth, he was weighed, and then remained quiet for several hours, after which time he was again weighed. The difference in the two weights indicated the amount of loss by pulmonary exhalation. Having taken off the air-tight dress, he was immediately weighed again, and a fourth time after a certain interval. The difference between the two weights last

ascertained, gave the amount of the cutaneous and pulmonary exhalation together; by subtracting from this the loss by pulmonary exhalation alone, while he was in the air-tight dress, he ascertained the amount of cutaneous transpiration. The repetition of these experiments during a long period, showed that during a state of rest, the average loss by cutaneous and pulmonary exhalation in a minute, is from seventeen to eighteen grains,—the minimum eleven grains, the maximum thirty-two grains; and that of the eighteen grains, eleven pass off by the skin, and seven by the lungs. The maximum loss by exhalation, cutaneous and pulmonary, in twenty-four hours, is 5lb.; the minimum, 1lb. 11oz. 4dr. (xlii. 1790). Valentin found the whole quantity lost by exhalation from the cutaneous and respiratory surfaces of a healthy man who consumed daily 40,000 grains of food and drink, to be 19,000 grains, or 3½lbs. Subtracting from this, for the pulmonary exhalation, 5,000 grains, and, for the excess of the weight of the exhaled carbonic acid over that of the equal volume of the inspired oxygen, 2,256 grains, the remainder, 11,744 grains, or about 2½lbs., may represent an average amount of cutaneous exhalation in the day.

The large quantity of watery vapour thus exhaled from the skin, will prove that the amount excreted by simple transudation through the cuticle must be very large, if we may take Krause's estimate of about eight square inches for the total evaporating surface of the sudoriparous glands; for not more than about 3,365 grains could be evaporated from such a surface in twenty-four hours, under the ordinary circumstances in which the surface of the skin is placed (xxv. 1843-4, p. 40). This estimate is not an improbable one, for it agrees very closely with that of Milne Edwards, who calculated that when the temperature of the atmosphere is not above 68° F., the glandular secretion of the skin contributes only $\frac{1}{6}$th to the total sum of cutaneous exhalation (xlvi).

The quantity of watery vapour lost by transpiration, is of course influenced by all external circumstances which affect

the exhalation from other evaporating surfaces, such as the temperature, the hygrometric state, and the stillness of the atmosphere. But, of the variations to which it is subject under the influence of these conditions, no calculation has been yet made.

Neither, until recently, has there been any estimate of the quantity of carbonic acid exhaled by the skin on an average, or in various circumstances. Regnault and Reiset have attempted to supply this defect, and conclude from some careful experiments that the quantity of carbonic acid generated by the body of a warm-blooded animal is about $\frac{1}{50}$th of that furnished by the pulmonary respiration (liii. 1849). The cutaneous exhalation is most abundant in the lower classes of animals, more particularly the naked Amphibia, as frogs and toads, whose skin is thin and moist, and readily permits an interchange of gases between the blood circulating in it and the surrounding atmosphere. Bischoff found that, after the lungs of frogs had been tied and cut out, about a quarter of a cubic inch of carbonic acid gas continued to be exhaled by the skin. And this quantity is very large, when it is remembered that a full-sized frog will generate only about half a cubic inch of carbonic acid by his lungs and skin together in six hours (Milne Edwards and Müller, xxxii. p. 328). That the respiratory function of the skin is, perhaps, even more considerable in the higher animals than appears to be the case from the experiments of Regnault and Reiset just alluded to, is made probable by the fact observed by Fourcault (xviii. March 1844), Magendie (xix. Dec. 1843), and others, that if the skin is covered with an impermeable varnish or the body inclosed, all but the head, in a caoutchouc dress, animals soon die, as if asphyxiated; their heart and lungs being gorged with blood, and their temperatures, during life, gradually falling many degrees, and sometimes as much as 36° F. below the ordinary standard (Magendie). Results so serious as these could not be consequent on the retention of water alone, for that might be discharged through the kidneys and lungs, or some other internal surface.

*Absorption by the Skin* has been already mentioned, as an instance in which that process is most actively accomplished. Metallic preparations rubbed into the skin have the same action as when given internally, only in a less degree. Mercury applied in this manner exerts its specific influence upon syphilis, and excites salivation; potassio-tartrate of antimony may excite vomiting, or an eruption extending over the whole body; and arsenic may produce poisonous effects. Vegetable matters also, if soluble, or already in solution, give rise to their peculiar effects, as carthartics, narcotics, and the like, when rubbed into the skin. The effect of rubbing is probably to convey the particles of the matter into the orifices of the glands, whence they are more readily absorbed than they would be through the epidermis. When simply left in contact with the skin, substances, unless in a fluid state, are seldom absorbed.

It has long been a contested question whether the skin covered with the epidermis has the power of absorbing water; and it is a point the more difficult to determine, because the skin loses water by evaporation. But, from the result of many experiments, it may now be regarded as a well-ascertained fact that such absorption really occurs. M. Edwards has proved that the absorption of water by the surface of the body may take place in the lower animals very rapidly. Not only frogs, which have a thin skin, but lizards, in which the cuticle is thicker than in man, after having lost weight by being kept for some time in a dry atmosphere, were found to recover both their weight and plumpness very rapidly when immersed in water. When merely the tail, posterior extremities, and posterior part of the body of the lizard were immersed, the water absorbed was distributed throughout the system (xlvi.). And a like absorption through the skin, though to a less extent, may take place also in man.

Dr. Madden having ascertained the loss of weight, by cutaneous and pulmonary transpiration, that occurred during half an hour in the air, entered the bath, and remained immersed during the same period of time, breathing through a tube which

communicated with the air exterior to the room. He was then carefully dried and again weighed. Twelve experiments were performed in this manner; and in ten there was a gain of weight, varying from 2 scruples to 5 drachms and 1 scruple, or a mean gain of 1 drachm 2 scruples and 13 grains. The loss in the air during the same length of time (half an hour) varied in ten experiments from $2\frac{1}{2}$ drachms to 1 ounce $2\frac{1}{2}$ scruples, or in the mean was about $6\frac{1}{2}$ drachms. So that, admitting the supposition that the cutaneous transpiration was entirely suspended, and estimating the loss by pulmonary exhalation at 3 drachms, there was, in these ten experiments of Dr. Madden, an average absorption of 4 drachms 1 scruple and 3 grains, by the surface of the body, during half an hour (xlvii.) In four experiments performed by M. Berthold, the gain in weight was greater than in those of Dr. Madden (lxxx. 1838, p. 177).

In severe cases of dysphagia, when not even fluids can be taken into the stomach, immersion in a bath of warm water or of milk and water may assuage the thirst: and it has been found in such cases that the weight of the body is increased by the immersion. Sailors, also, when destitute of fresh water, find their urgent thirst allayed by soaking their clothes in salt water and wearing them in that state; but these effects may be in part due to the hindrance to the evaporation of water from the skin.

The absorption, also, of different kinds of gas by the skin is proved by the experiments of Abernethy, Cruikshank, Beddoes, and others. In these cases, of course, the absorbed gases combine with the fluids, and lose the gaseous form. Several physiologists have observed an absorption of nitrogen by the skin: Beddoes says, that he saw the arm of a negro become pale for a short time when immersed in chlorine; and Abernethy observed that when he held his hands in oxygen, nitrogen, carbonic acid, and other gases contained in jars over mercury, the volume of the gases became considerably diminished.

The share which the evaporation from the skin has in the maintenance of the uniform temperature of the body, and the necessary adaptation thereto of the production of heat, has been already mentioned (p. 181).

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## CHAPTER XIV.

### THE KIDNEYS AND THEIR SECRETION.

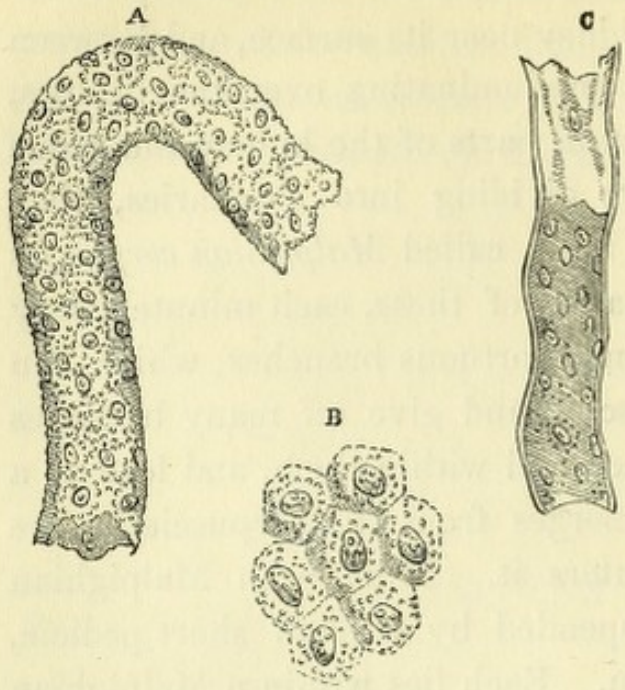
#### *Structure of the Kidneys.*

THE kidneys, provided especially for the excretion of the refuse nitrogen, phosphorus and sulphur, lime and magnesia, have the general structures of glands arranged in a manner distinguishing them from all other excretory organs. In each kidney numerous secreting tubes (*tubuli uriniferi*) are collected in bundles, in from ten to twenty separated conical or pyramidal portions (*pyramids* or *cones of Malpighi*), which together constitute the tubular portion of the kidney. The apices of the cones converge, and project into *calyces*, which are branches of a large cavity called the *pelvis* of the kidney, that leads to the ureter, its excretory duct. The trunks of the urine-tubes open at the extremities or *papillæ* of the pyramids and their branches running in a straight and somewhat divergent course towards the surface of the kidney, as they approach it, become tortuous, and, winding in various directions, terminate in, or bear on small pedicles proceeding from their walls, dilated, flask-shaped sacculi, named *capsules of Malpighi*. Those that bear capsules at their sides, probably unite with one another in loops, or terminate in simply closed ends.

The small branches of the renal arteries ramify very abundantly in the parts of the kidney near its surface, and between the several pyramids; and predominating over the tubules, have obtained for these *cortical* parts of the kidney the name of *vascular portion*. Before dividing into capillaries, they form vascular tufts or little balls, called *Malpighian corpuscles* or *glomerules*. In the formation of these, each minute artery divides into four or more small tortuous branches, which run on the surface of the corpuscles, and give off many branches that fill up the spaces between and within them, and lead to a small vein which usually emerges from the corpuscle at the same part as the artery enters it. Thus, each Malpighian corpuscle appears as if suspended by a small short pedicle, formed of its artery and vein. Each lies within a Malpighian capsule, or attached to its exterior (Hyrtl, lxxxviii. April, 1846; Bidder, lxxx. 1845), and from the vein of each proceed capillaries, which ramify in close networks over the urine-tubes. Thus, therefore, the circulation of the kidney is peculiar in that the capillaries, from which the blood is chiefly derived to form the urine, are like the divisions of a vein rather than of an artery: for the branchings of the arteries in the Malpighian tufts or corpuscles, and the collection of their branches again into the small efferent vessel, give that vessel the character of a vein, and make the capillary circulation over the urine-tubes, analogous to the portal circulation through the liver; an analogy which is the closer, because in fish and Amphibia the kidney receives not only a renal artery, whose branches form the Malpighian bodies, but also a large renal (or *renal-portal*) vein, bringing, for the secretion of urine, the venous blood of the hinder parts of the body, and giving off the capillaries which ramify upon the urine-tubes (Bowman, xliii., 1842).

The urine-tubes are minute canals of about $\frac{1}{700}$th of an inch in diameter, formed of pellucid, simple, or basement-membrane and lined throughout with nucleated gland cells, arranged like an epithelium, of spheroidal form, and darkly dotted or

*Fig.* 41.*




granulated (see fig. 41). Not unfrequently, portions of tubes, especially of those that are convoluted or tortuous, appear nearly filled with such cells, or thin separated nuclei, as if the urine were filtered through them on its way to the pelvis. The same kind of epithelium is continued into the Malpighian capsules, and lines their whole internal surface, and if they contain Malpighian tufts, is reflected over them like a serous membrane.†

## *Secretion of Urine.*

The separation of urine from the blood is probably effected, like other secretions, by the agency of the gland cells, and equally in all parts of the urine-tubes. The urea and uric acid, and perhaps some of the other constituents existing

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* Fig. 41. A. Portion of a secreting canal from the cortical substance of the kidney. B. The epithelium or gland cells, more highly magnified (700 times). C. Portion of a canal from the medullary substance of the kidney. At one part the basement-membrane has no epithelium lining it.

† In the frog, triton, and probably most or all other naked Amphibia, the epithelium at, and just within, the neck or commencing dilatation of the Malpighian capsule is ciliated. This fact (first observed by Mr. Bowman) is, perhaps, connected with the peculiar arrangement of the seminal tubes or branches of the vasa deferentia, which open into one end of the Malpighian capsules, while the urine-tubes open into the others. The cilia work towards the seminal tubes, and would prevent the seminal fluid from mingling with the urine (see Bidder, cliv., and Ludwig, lix. 1847).

ready formed in the blood, may need only separation, that is, they may pass from the blood to the urine without further elaboration; but this is not the case with some of the other principles of the urine, such as the acid phosphates and the sulphates, for these salts do not exist in the blood, and must be formed by the chemical agency of the cells.

The large size of the renal arteries and veins permits so rapid a transit of the blood through the kidneys, that the whole of the blood is purified by them. The secretion of urine is rapid in comparison with other secretions, and as each portion is secreted, it propels those already in the tubes onwards into the pelvis. Thence through the ureter the urine passes into the bladder, into which its rate and mode of entrance has been watched in cases of ectopia vesicæ, *i. e.*, of such fissures in the anterior and lower part of the walls of the abdomen, and of the front wall of the bladder, that its hinder wall with the orifices of the ureters is exposed to view. Some good observations on such cases were made by Mr. Erichsen (lxxi. 1845). The urine does not enter the bladder at any regular rate, nor is there a synchronism in its movement through the two ureters. During fasting, two or three drops enter the bladder every minute, each drop as it enters first raising up the little papilla on which, in these cases, the ureter opens, and then passing slowly through its orifice, which at once again closes like a sphincter. In the recumbent posture, the urine collects for a little time in the ureters, then flows gently, and if the body be raised, runs from them in a stream till they are empty. Its flow is increased in deep inspiration, or straining, and in active exercise, and in fifteen or twenty minutes after a meal.

The same observations, also, shewed how fast some substances pass from the stomach through the circulation, and through the vessels of the kidneys. Ferrocyanide of potassium so passed on one occasion in a minute: vegetable substances, such as rhubarb, occupied from sixteen to thirty-five minutes; neutral alkaline salts with vegetable bases, which were gene-

rally decomposed *in transitu*, made the urine alkaline in from twenty-eight to forty-seven minutes. But the times of passage varied much; and the transit was always slow when the substances were taken during digestion.

The urine collecting in the urinary bladder is prevented from regurgitation into the ureters by the mode in which they pass through the walls of the bladder, namely, by their lying for between half and three-quarters of an inch between the muscular and mucous coats, and then turning rather abruptly forwards, and opening through the latter. It collects till the distension of the bladder is felt either by direct sensation, or, in ordinary cases, by a transferred sensation at and near the orifice of the urethra. Then, the effort of the will being directed primarily to the muscles of the abdomen, and through them (by reason of its tendency to act with them), to the urinary bladder, the latter, though its muscular walls are really composed of involuntary muscle, contracts, and expels the urine. The muscular fibres behind the ureters, where they lie between the muscular and mucous coats of the bladder, compress these canals as they contract for the expulsion of the urine; and the vesical orifice of the urethra, which appears to be closed only by the elasticity of the surrounding parts, is forced open by the pressure of the urine while the bladder is contracting, and again closes by the same elasticity when the bladder ceases to contract.

## *The Urine: its general Properties.*

Healthy urine is a clear limpid fluid, of a pale yellow or amber colour, with a peculiar faint aromatic odour, which becomes pungent and ammoniacal when decomposition takes place. The urine, though usually clear and transparent at first, often, as it cools, becomes opaque and turbid from the deposition of part of its constituents previously held in solution; and this may be consistent with health, though it is

only in disease that, in the temperature of 98° or 100°, at which it is voided, the urine is turbid even when first expelled. Although ordinarily of a pale amber colour, yet, consistently with health, the urine may be nearly colourless, or of a brownish or deep orange tint; and between these extremes, it may present every shade of colour.

When secreted, and most commonly, when first voided, the urine has a distinctly acid reaction in man and all carnivorous animals, and it thus remains till it is neutralized or made alkaline by the ammonia developed in it by decomposition. In most herbivorous animals, on the contrary, the urine is alkaline and turbid. The difference depends, not on any peculiarity in the mode of secretion, but on the differences in the food on which the two classes subsist; for when carnivorous animals, such as dogs, are restricted to a vegetable diet, their urine becomes pale, turbid, and alkaline, like that of an herbivorous animal, but resumes its former acidity on the return to an animal diet; while the urine voided by herbivorous animals, *e. g.*, rabbits, fed for some time exclusively upon animal substances, presents the acid reaction and other qualities of the urine of Carnivora, its ordinary alkalinity being restored only on the substitution of a vegetable for the animal diet (Bernard, xviii. 1846). Human urine is not usually rendered alkaline by vegetable diet, but it becomes so after the free use of alkaline medicines, or of the alkaline salts with carbonic or vegetable acids; for these latter are changed into alkaline carbonates previous to elimination by the kidneys. Except in these cases it is very rarely alkaline, unless ammonia has been developed in it by decomposition commencing before it is evacuated from the bladder.

The average *specific gravity* of the human urine is stated by Dr. Prout to be 1020 (xxi. p. 518), by Becquerel, as the mean in the two sexes, 1017 (M. p. 148).* Probably no other animal

* The specific gravity indicates only the proportionate, not the absolute quantity of solid matter in a given bulk of urine. For determining

fluid presents so many varieties in density within twenty-four hours as the urine does; for the relative quantity of water and of solid constituents of which it is composed is materially influenced by the condition and occupation of the body during the time at which it is secreted, by the length of time which has elapsed since the last meal, and by several other accidental circumstances. The existence of these causes of difference in the composition of the urine has led to the secretion being described under the three heads of *urina sanguinis*, *urina potûs*, and *urina cibi*. The first of these names signifies the urine, or that part of it which is secreted from the blood at times in which neither food nor drink has been recently taken, and is applied especially to the urine which is evacuated in the morning before breakfast. The *urina potûs* indicates the urine secreted shortly after the introduction of any considerable quantity of fluid into the body: and the *urina cibi* the portions secreted during the period immediately succeeding a meal of solid food. The last kind contains a larger quantity of solid matter than either of the others; the first or second, being largely diluted with water, possesses a comparatively low specific gravity. Of these three kinds, the morning-urine is the best calculated for analysis, since it represents the simple secretion unmixed with the elements of food or drink; if it be not used, the whole of the urine passed during a period of twenty-four hours should be taken. In accordance with the various circumstances above-mentioned, the specific gravity of the urine may, consistently with health, range widely on both sides of the usual average. The average healthy range may be stated at from 1015 in the winter to 1025 in the summer (Prout, xxi. p. 518), and variations of diet and exercise may make as great a difference. In disease, the variation may be greater; sometimes descending, in albuminuria, to 1004, and fre-

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the latter point, various tables have been constructed; see Christison, xlix. vol. iv. p. 248; Becquerel, L. p. 17; Prout, xxi. p. 251; Day, xxx. 1844, p. 370; and Golding Bird, li. p. 17.

quently ascending, in diabetes, when the urine is loaded with sugar, to 1050, or even to 1060 (Watson, xlviii. vol. ii. p. 557).

The whole *quantity* of urine secreted in twenty-four hours is subject to variation according to the amount of fluid drunk, and the proportion secreted by the skin. It is because the secretion of the skin is more active in summer than in winter, that the quantity of urine is smaller, and its specific gravity proportionately higher. According to Prout, the quantity voided in summer may be estimated at 30 ounces daily; that in winter at 40 ounces: this will give a mean of 35 ounces as the average amount of the urinary secretion by an adult healthy man.

### *Chemical Composition of the Urine.*

The urine consists of water, holding in solution certain animal and saline matters as its ordinary constituents, and occasionally various matters taken into the stomach as food—salts, colouring matter, and the like. The quantities of the several natural and constant ingredients of the urine are stated somewhat differently by the different chemists who have analysed it; but many of the differences are not important, and the well-known accuracy of the several chemists renders it almost immaterial which of the analyses is adopted. The analysis by A. Becquerel (L. p. 7) being adopted by Dr. Prout (xxi. p. 519), and by Dr. Golding Bird (li. p. 31), will be here employed. The older analysis by Berzelius (xxiv. p. 432), adopted by Müller (xxxii. p. 631), includes all the principal solid constituents of the urine, and probably states correctly the proportions that they bear to one another; but, as pointed out by Dr. Prout, it is probable that Berzelius examined urine of very high specific gravity, and has, in consequence, overstated the quantity of solid ingredients; for he sets them down at more than double the amount found to exist by more recent analysts. If the mean specific gravity

of human urine be taken at 1020, and the average quantity passed in twenty-four hours be estimated at thirty-five ounces, it will be found, according to the analysis of M. Becquerel, that 1000 parts of urine contain 33 parts of solid matter dissolved in 967 parts of water. Its more exact composition is as follows:—

| | | | |
|---|---|---|---|
| Water | | | 967· |
| Urea | | | 14·230 |
| Uric acid | | | ·468 |
| Colouring matter, Mucus, and animal extractive matter | inseparable from each other | | 10.167 |
| Salts | Sulphates | Soda, Potash | 8.135 |
| | Bi-phosphates | Lime, Soda, Magnesia, Ammonia | |
| | Chlorides | Sodium, Potassium | |
| | Hippurate of soda | | |
| | Fluoride of potassium | | |
| Silica | | | traces. |
| | | | 1000·000 |

From these proportions, however, most of the constituents are, even in health, liable to variations. Especially, the *water* is so. Its variations in different seasons, and according to the quantity of drink and exercise have already been mentioned. It is also liable to be influenced by the condition of the nervous system, being sometimes greatly increased in hysteria, and some other nervous affections; and at other times diminished. In some diseases it is enormously increased; and its increase may be either attended with an augmented quantity of solid matter, as in ordinary diabetes, or may be nearly the sole change, as in the affection termed diabetes insipidus. In other diseases, *e.g.*, the various forms of albuminuria, the quantity may be considerably diminished. A febrile condition almost always diminishes the quantity of water; and a like diminution is caused by any affection which draws off

a large quantity of fluid from the body through any other channel than that of the kidneys, *e.g.*, the bowels and the skin.

*Urea.*—Urea is the principal solid constituent of the urine, forming nearly one-half of the whole quantity of solid matter. It is also the most important ingredient, since it is the chief substance by which the nitrogen of decomposed tissues and superfluous food is excreted from the body. For its removal, the secretion of urine seems especially provided; and by its retention in the blood the most pernicious effects are produced.

Urea, like the other solid constituents of the urine, exists in a state of solution. But it may be procured in the solid state, and then appears in the form of delicate silvery acicular crystals, which, under the microscope, appear as four-sided prisms. It is obtained in this state by evaporating urine carefully to the consistence of honey, acting on the inspissated mass with four parts of alcohol, then evaporating the alcoholic solution, and purifying the residue by repeated solution in water or alcohol, and finally allowing it to crystallise. It readily combines with an acid, like a weak base; and may thus be conveniently procured in the form of a nitrate, by adding about half a drachm of pure nitric acid to double that quantity of urine in a watch-glass. The crystals of nitrate of urea are formed more rapidly if the urine have been previously concentrated by evaporation.

Urea is colourless when pure; when impure, yellow or brown: without smell, and of a cooling, nitre-like taste; has neither an acid nor an alkaline re-action, and deliquesces in a moist and warm atmosphere. At 59° F. it requires for its solution less than its weight of water; it is dissolved in all proportions by boiling water; but it requires five times its weight of cold alcohol for its solution. At 248° F. it melts without undergoing decomposition; at a still higher temperature ebullition takes place, and carbonate of ammonia sublimes; the melting mass gradually acquires a pulpy consistence; and, if the heat is carefully regulated, leaves a grey-white powder, cyanic acid.

Urea is identical in composition with cyanate of ammonia, its ultimate analysis yielding 2 atoms of carbon, 2 of nitrogen, 2 of oxygen, and 4 of hydrogen, which is the composition of hydrated cyanate of ammonia (cyanic acid=$C_2NO$; water=HO; ammonia=$NH_3$). This cyanate of ammonia, or artificial urea, as discovered by Wöhler, may be formed by the mutual action of ammonia, cyanic acid, and water; or by decomposing cyanate of silver with hydrochlorate of ammonia, or cyanate of lead with a solution of ammonia (liii. xxvii. 196). The action of heat upon urea in evolving carbonate of ammonia, and leaving cyanic acid, is thus explained. A similar decomposition of the urea with development of carbonate of ammonia ensues spontaneously when urine is kept for some days after being voided, and explains the ammoniacal odour then evolved. It is probable, that this spontaneous decomposition is accelerated by the mucus and other animal matters in the urine, which, by becoming putrid, act the part of a ferment and excite a change of composition in the surrounding compounds. It is chiefly thus that the urea is sometimes decomposed before it leaves the bladder, when the mucous membrane is diseased, and the mucus secreted by it is both more abundant and, probably, more prone than usual to become putrid (Dumas, lii. p. 39). The same occurs also in some affections of the nervous system, particularly in paraplegia.

Assuming 35 ounces of urine to be passed in twenty-four hours, the total amount of urea excreted within the same period, at the rate of fourteen parts and a quarter in every 1000 parts of urine, will be 239 grains and a fraction, or nearly half an ounce (Prout). Dr. Thudichum estimates the daily normal amount much higher (ccxxiii). The quantity excreted is, however, like that of the urine itself, subject to considerable variation. It is materially influenced by diet, being greater when animal food is exclusively used, less when the diet is mixed, and least of all with a vegetable diet (Lehmann, lxxxii. vol. ii. p. 162). As a rule, men excrete a larger quantity than women, and persons in the middle periods

of life, a larger quantity than infants or old people (Lecanu, lvi. t. 25, p. 261). The quantity of urea does not necessarily increase and decrease with that of the urine, though on the whole it would seem that whenever the amount of urine is much augmented, the quantity of urea also is usually increased (Becquerel, L.). In various diseases, as albumiuaria, the quantity is reduced considerably below the healthy standard, while in other affections it is above it.

The urea appears to be derived from two different sources. That it is derived in part from the unassimilated elements of nitrogenous food, circulating with the blood, is shown in the increase which ensues on substituting an animal or highly nitrogenous, for a vegetable diet (see especially Lehmann, cciii. vol. ii. pp. 450—2). And that it is in larger part derived from the disintegratiou of the azotized animal tissues, is shown by the fact that it continues to be excreted, though in smaller quantity than usual, when all nitrogenous substances are strictly excluded from the food, as when the diet consists for several days of sugar, starch, gum, oil, and similar non-azotized vegetable substances (Lehmann, loc. cit., and lxxxii. vol. ii. p. 163; and Bischoff, ccxvi.). It is excreted also even although no food at all be taken for a considerable time; thus it is found in the urine of reptiles which have fasted for months; and in the urine of a madman who had fasted eighteen days, Lassaigne found both urea and all the components of healthy urine (lvii. p. 272). For these and other reasons, Bischoff believes that urea is exclusively derived from the metamorphosis of tissues, and that no part of it is furnished by unassimilated elements of food. According to Dr. Prout (xxi. p. 483), the urea is derived chiefly from the gelatinous tissues; according to Liebig (xi. p. 137), all the nitrogenous tissues furnish a share of it by their decomposition; that the muscles do so is nearly proved by the close relation between urea and the kreatine and the kreatinine, which both they and urine contain, and by the increased excretion of urea after active exercise.

Urea exists ready-formed in the blood, and is simply abstracted therefrom by the kidneys. It may be detected in small quantity in the blood (ix. 1848), and in some other parts of the body, *e. g.*, the humours of the eye (Millon, xviii. 1843), even while the functions of the kidneys are unimpaired: but when from any cause, especially extensive disease or extirpation of the kidneys, the separation of urine is imperfect, the urea is found largely in the blood and most other fluids of the body.

*Uric Acid.*—This, which is another nitrogenous animal substance, and was formerly termed lithic acid on account of its existence in many forms of urinary calculi, is rarely absent from the urine of man or animals, though in the feline tribe it seems to be sometimes entirely replaced by urea (G. Bird, lxxi. vol. xli. p. 1106). Its proportionate quantity varies considerably in different animals. In man, and Mammalia generally, especially the Herbivora, it is comparatively small, not exceeding, in the human subject, one part in 2000 parts of urine. According to Thudichum, about 8 grains is the average daily quantity excreted in human urine. In the whole tribe of birds and of serpents, on the other hand, the quantity is very large, greatly exceeding that of the urea. In the urine of graminivorous birds, indeed, urea is rarely if ever found, its place being entirely supplied by uric acid. The quantity of uric acid, like that of urea, in human urine, is increased by the use of animal food, and decreased by the use of food free from nitrogen, or by an exclusively vegetable diet. In most febrile diseases, and in plethora, it is formed in unnaturally large quantities; and in gout it is deposited in, and in the tissues around, joints, in the form of urate of soda, of which the so-called chalk-stones of this disease are principally composed.

The condition in which uric acid exists in solution in the urine, has formed the subject of much discussion, because of its difficult solubility in water. Dr. Prout found that it required 10,000 times its weight of water, at the temperature of 60° F. for solution; whereas in urine, one part of it is retained in

solution by only 2,000 parts of water. He was led to believe that uric acid does not exist in the free state in urine, but is combined with ammonia in the form of the more soluble salt of urate of ammonia. This view is supported by the fact, that urine, when evaporated, deposits not crystals of uric acid, as would probably be the case if this acid existed in its free state, but urate of ammonia. It is supported also by the facts, that the addition of an acid to urine causes the deposition of crystals of uric acid, and that the uric acid in the excrement of birds and serpents is not in the free state, but is combined with ammonia. It may therefore be considered highly probable that the principal part at least of the uric acid exists in the urine, in the form of urate of ammonia; and Dr. Bence Jones has shown that the solubility of this salt is increased by the presence of chloride of sodium, of which a proportion is present in the urine (lxxi. Dec. 1843).)

According to Liebig (xxx. June, 1844), however, the uric acid exists as urate of soda, produced, he supposes, by the uric acid, as soon as it is formed, combining with part of the base of the alkaline phosphate of soda of the blood. Hippuric acid, which exists in human urine also, he believes, acts upon the alkaline phosphate in the same way, and increases still more the quantity of acid phosphate, on the presence of which it is probable that a part of the natural acidity of the urine depends. It is scarcely possible to say whether the union of uric acid with the bases soda and ammonia, takes place in the blood, or in the act of secretion in the kidney: the latter is the more probable opinion, but the quantity of either uric acid or urates in the blood, is probably too small to allow of this question being solved.

According to Dr. Prout, the source of uric acid is in the disintegrated elements of albuminous tissues: while by Liebig it is assumed that uric acid is the first-formed product of the decay of all azotized tissues, and that if a due supply of oxygen is afforded, it is resolved into urea and carbonic acid. The fact, however, that in birds, whose rapid respiration and

circulation ensures a large supply of oxygen, the uric acid is excreted in the form of urate of ammonia, and is rarely converted into urea, is quite opposed to such a view. The relation which uric acid and urea bear to each other, is therefore still obscure. The fact that they often exist together in the same urine, makes it seem probable that they have different origins or different offices to perform: but the entire replacement of either by the other, as of urea by uric acid in the urine of birds, serpents, and many insects, and of uric acid by urea, in the urine of the feline tribe of Mammalia, shews that each alone may discharge all the important functions of the two.

Owing to its existing in combination in healthy urine, uric acid, for examination, must generally be precipitated from its bases by a stronger acid. Frequently, however, when excreted in excess, it is deposited in a crystalline form, mixed with large quantities of urate of ammonia or soda. In such cases it may be procured for microscopic examination, by gently warming the portion of urine containing the sediment: this dissolves urate of ammonia and soda, while the comparatively insoluble crystals of uric acid subside to the bottom. In larger quantity, this acid may be obtained from the urine of birds or serpents, which consists almost exclusively of urate of ammonia. The thick, white, urinary secretion of these animals is to be dried, dissolved in warm water, filtered, and then decomposed with nitric or hydrochloric acid.

The most common form in which uric acid is deposited in urine, is that of a brownish or yellowish powdery substance, consisting of granules of urate of ammonia or soda. When deposited in crystals, it is most frequently in rhombic or diamond-shaped laminæ, not unlike scales of epithelium, their resemblance to which is often further increased by the existence of internal markings, which look like nuclei. The laminæ are sometimes of considerable thickness; and, when lying on their sides, they often appear like flattened cylinders; but their true form is made manifest as they roll over. Occa-

sionally the rhombic form of the crystals is replaced by the square. Various other shapes are occasionally presented, and will be found described in works on the subject (see especially Prout xxi.; G. Bird, li.; Simon, lxxxii.; Griffith, cii.). When deposited from urine, the crystals are generally more or less deeply coloured, by being combined with the colouring principles of the urine.

Uric acid is insoluble in ether and alcohol. It contains about 31 per cent. of nitrogen; its analysis yielding, according to Dr. Prout, nitrogen 31·12, carbon 39·87, hydrogen 2·22, oxygen 26·27. Its formula is $C_{10}H_4N_4O_6$.

*Hippuric Acid* has long been known to exist in the urine of herbivorous animals in combination with soda. Liebig has shown that it also exists naturally in the urine of man, in quantity equal to the uric acid (xxx. June 1844), and Weismann's observations agree with this (xxxiii. 3 Ser. p. 337); but, according to Dr. G. Bird, its quantity is not more than one-third of the uric acid. It is a nitrogenous compound, and contains as much as 63 per cent. of carbon; 100 parts, according to Liebig, consisting of C 63·032, H 5·000, N 7·337, O 24·631. It is closely allied to benzoic acid; and this substance when introduced into the system, is excreted by the kidneys, as hippuric acid (Ure, xli. vol. xxiv). Its source is not satisfactorily determined: in part it is probably derived from some constituents of vegetable diet, though man has no hippuric acid in his food, nor, commonly, any benzoic acid, that might be converted into it; in part from the natural disintegration of tissues, independent of vegetable food, for Weismann constantly found an appreciable quantity, even when living on an exclusively animal diet. By some it is thought to be derived from the glycine of the bile.

The nature and composition of the *colouring matter* of urine is involved in considerable obscurity. It is usually supposed that there are two distinct kinds, a yellow and a red, by the varying proportions of which the different tints of urine are produced. (See on the subject G. Bird, li. p. 52; Heller, ix.

1846-7; Simon, lxxxii.; Thudichum, ccxxiii.; and, for a full account, Scherer, x. Bd. 57, p. 180, or for an abstract of the paper there given, lix. 1846, p. 130).

The *mucus* in the urine consists principally of the epithelial débris of the mucous surface of the urinary passages. Particles of epithelium, in greater or less abundance, may be detected in most samples of urine, especially if it has remained at rest for some time, and the lower strata are then examined. As urine cools, the mucus is sometimes seen suspended in it as a delicate opaque cloud, but generally it falls. In inflammatory affections of the urinary passages, especially of the bladder, mucus in large quantities is poured forth, and speedily undergoes decomposition. The presence of the decomposing mucus excites (as already stated) chemical changes in the urea, whereby ammonia, or carbonate of ammonia, is formed, which, combining with the excess of acid in the super-phosphates in the urine, produces insoluble neutral or alkaline phosphates of lime and magnesia, and phosphate of ammonia and magnesia. These, mixing with the mucus, constitute the peculiar white, viscid, mortar-like substance which collects upon the mucous surface of the bladder, and is often passed with the urine, forming a thick, tenacious sediment.

Besides mucus and colouring matter, urine contains a considerable quantity of animal matter, usually described under the obscure name of *animal extractive*. The investigations of Liebig (liv,), Heintz (lix. 1847, p. 105), and others, have shewn that some of this ill-defined substance consists of *kreatine* and *kreatinine*, two crystallizable substances derived from the metamorphosis of muscular tissue. These substances appear to be intermediate between the proper elements of the muscles, and perhaps of other azotized tissues, and urea: the first products of the disintegrating tissues probably consisting not of urea, but of kreatine and kreatinine which subsequently are partly resolved into urea, partly discharged, without change, in the urine. Scherer's analysis shows also, that much of the substance classed as extractive matter of the urine, is a pecu-

liar colouring matter, probably derived from the hæmatine of the blood.

*Salts.*—The saline substances in urine constitute about one-fourth of the solid ingredients. They consist of the various saline matters found in the other fluids and tissues of the body, together with some that are peculiar to the urine.

The *Sulphates* are the most abundant; they exist as the sulphates of soda and potash: salts which are taken in very small quantity with the food, and are scarcely found in other fluids or tissues of the body; for the sulphates commonly enumerated among the constituents of the ashes of the tissues and fluids are, for the most part or entirely, produced by the changes that take place in the burning. Hence it is probable that the sulphuric acid which the sulphates in the urine contain, as soon as it is formed in the blood, or in the act of secretion of urine, is combined with the soda and potash which are in excess in the blood, and make it alkaline. The sulphur of which the acid is formed, is probably derived from the decomposing nitrogenous tissues, the other elements of which are resolved into urea and uric acid. The oxygen is supplied through the lungs, and the heat generated during combination with the sulphur, is one of the subordinate means by which the animal temperature is maintained.

Besides the sulphur in these salts, some also appears to be in the urine, uncombined with oxygen; for after all the sulphates have been removed from urine, sulphuric acid may be formed by drying and burning it with nitre. Mr. Ronalds believes that from three to five grains of sulphur are thus daily excreted (xvii. 1846). The combination in which it exists is uncertain: possibly it is in some compound analogous to cystine or cystic oxyde, which contains as much as 25 per cent. of sulphur.

*The Phosphates* are more numerous, though less abundant, than the sulphates. From $\frac{1}{4}$th to $\frac{1}{18}$th part of them are phosphates with alkaline bases; from $\frac{3}{4}$ths to $\frac{17}{18}$ths, with earthy

bases (Bence Jones, xliii. 1845). In blood, saliva, and other alkaline fluids of the body, phosphates exist in the form of alkaline, probably tribasic, salts. In the urine they are acid salts, viz., the bi-phosphates of soda, ammonia, lime, and magnesia, the excess of acid being, according to Liebig (xxx. June 1844), due to the appropriation of the alkali with which the phosphoric acid in the blood is combined, by the several new acids which are formed or discharged at the kidneys, namely, the uric, hippuric, and sulphuric acids, all of which he supposes to be neutralized with soda.

The presence of the acid phosphates accounts, in great measure, or, according to Liebig, entirely, for the acidity of the urine. The phosphates are taken largely in both vegetable and animal food; some, thus taken, are excreted at once; others, after being transformed and incorporated with the tissues. Phosphate of lime forms the principal earthy constituent of bone, and from the decomposition of the osseous tissue the urine derives a large quantity of this salt. The decomposition of other tissues also, but especially of the brain and nerve-substance, furnishes large supplies of phosphorus to the urine, which phosphorus is supposed, like the sulphur, to be united with oxygen, and then combined with bases. According to Becquerel, 1000 parts of urine contain on an average ·373 of phosphoric acid in the state of combination; so that a person in health will pass about 6·26 grains in twenty-four hours. This quantity is, however, liable to considerable variation. Any undue exercise of the mind, and all circumstances producing nervous exhaustion, increase it. The earthy phosphates are more abundant after meals, whether on animal or vegetable food, and are diminished after long fasting. The alkaline phosphates are increased after animal food, diminished after vegetable food. Exercise increases the alkaline, but not the earthy phosphates (Bence Jones). Phosphorus uncombined with oxygen appears, like sulphur, to be excreted in the urine (Ronalds, l. c.), and it is said that the

quantity is sometimes so large as to render objects dipped in the urine luminous in the dark.

The *Chlorides* occur as chlorides of potassium and sodium. As they exist largely in food, and in most of the animal fluids, their occurrence in the urine is easily understood. Occasionally the urine contains *fluate of potash*, and a small quantity of *silica*; but neither of these appears to be a constant constituent.*

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## CHAPTER XV.

### THE NERVOUS SYSTEM.

THE general nature of the functions of the nervous system, its connection with the mind on the one hand, and the contractile and sensitive parts on the other, and its influence on the functions of organic life, have been already referred to (pp. 32—34). The following pages will be devoted to a fuller exposition of these subjects.

The nervous system consists of two portions or constituent systems, the *cerebro-spinal*, and the *sympathetic* or *ganglionic*, each of which (though they have many things in common)

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* In addition to the various works already quoted, see, for further details on the Chemistry of the Urine, Dr. Garrod's lectures in the Lancet for 1848; Dr. Golding Bird's lectures in the forty-second volume of the Medical Gazette; Dr. Day's several reports in Ranking's Abstract, and in the British and Foreign Medico-Chirurgical Review; Scherer's Reports in Canstatt's Jahresberichte to 1860; and among others the works of Dr. Griffith (cii.), Dr. Bence Jones (cxcviii.), J. E. Bowman (ccxv.), Lehmann (cciii. and ccxxi.), and Thudichum (ccxxiii.)

possesses certain peculiarities in structure, mode of action, and range of influence.

The *cerebro-spinal* system includes the brain and spinal cord, with the nerves proceeding from them, and the several ganglia seated upon these nerves, or forming part of the substance of the brain. It was denominated by Bichat the nervous system of animal life; and includes all the nervous organs in and through which are performed the several functions with which the mind is more immediately connected; namely, those relating to sensation and volition, and the mental acts connected with sensible things.

The *sympathetic* or *ganglionic* portion of the nervous system, which Bichat named the nervous system of organic life, consists essentially of a chain of ganglia connected by nervous cords, which extend from the cranium to the pelvis, along each side of the vertebral column, and from which nerves with ganglia proceed to the viscera in the thoracic, abdominal, and pelvic cavities. By its distribution, as well as by its peculiar mode of action, this system is less immediately connected with the mind, either as sensiferous or as receiving the impulses of the will; it is more closely connected than the cerebro-spinal system is with the processes of organic life.

But the differences between these two systems are not essential: their actions differ in degree and object more than in kind or mode: in the lower animals all the nervous functions are performed by one system corresponding with the cerebro-spinal of the Vertebrata; and among the Vertebrata many of the functions which, in the warm-blooded animals, are controlled by the sympathetic nerves, are in fish under the control of the pneumogastric cerebral nerves.

### *Elementary Structures of the Nervous System.*

The organs of the nervous system, or systems, are composed essentially of two kinds of structure, vesicular and fibrous;

both of which appear essential to the construction of even the simplest nervous system. The vesicular structure is usually collected in masses and mingled with the fibrous structure, as in the brain, spinal cord, and the several ganglia; and these masses constitute what are termed *nervous centres*, being the organs in which it is supposed that nervous force may be generated, and in which are accomplished all the various reflections, and other modes of disposing of impressions when they are not simply conducted along nerve-fibres. The fibrous nerve-substance, besides entering into the composition of the nervous centres, forms alone the *nerves*, or cords of communication, which connect the various nervous centres, and are distributed in the several parts of the body for the purpose of conveying nervous force to them, or of transmitting to the nervous centres the impressions made by stimuli.

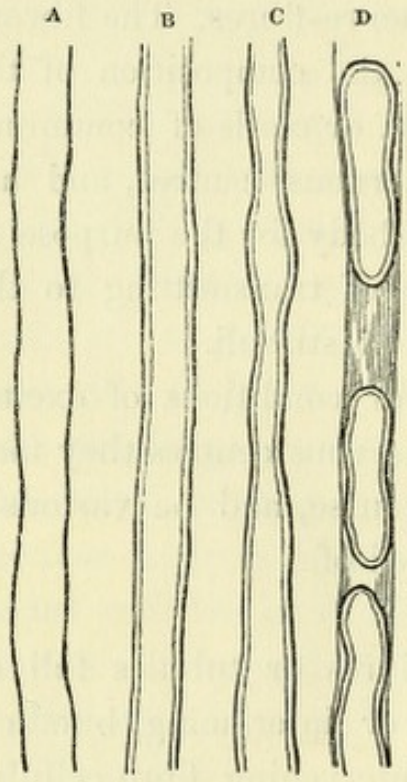
Along the nerve-fibres impressions or conditions of excitement are simply conducted: in the nervous centres they may be made to deviate from their direct course, and be variously diffused, reflected, or otherwise disposed of.

*Nerves* are constructed of minute fibres or tubules full of nervous matter, arranged in parallel or interlacing bundles, which bundles are connected by intervening fibro-cellular tissue, in which their principal blood-vessels ramify. A layer of the same, or of strong fibrous tissue also surrounds the whole nerve, and forms a sheath or neurilemma for it. In most nerves, two kinds of fibres are mingled; those of one kind being most numerous in, and characteristic of, nerves of the cerebro-spinal system; those of the other, most numerous in nerves of the sympathetic system.

The fibres of the first kind appear to consist of tubules of a pellucid simple membrane, within which is contained the proper nerve substance, consisting of transparent, oil-like, and apparently homogeneous material, which gives to each fibre the appearance of a fine glass tube filled with a clear transparent fluid (fig. 42A). This simplicity of composition,

is, however, only apparent in the fibres of a perfectly fresh nerve; for, shortly after death, they undergo changes which make it probable that their contents are composed of two different materials. The internal, or central part, occupying the axis of the tube, becomes greyish, while the outer, or cortical portion, becomes opaque and dimly granular, or grumous, as if from a kind of coagulation. At the same time, the fine outline of the previously transparent cylindrical tube is exchanged for a dark double contour (fig. 42, B), the outer line being formed by the sheath of the fibre, the inner by the margin of curdled or coagulated medullary substance. The granular material shortly collects into little masses, which distend portions of the tubular membrane, while the intermediate spaces collapse, giving the fibres a varicose, or beaded appearance (fig. 42, C and D), instead of their previous cylindrical form.

*Fig.* 42*.




The difference produced in the contents of the nerve-fibres when exposed to the same conditions, has, with other facts, led to the opinion, now generally adopted, that the central part of each nerve-fibre differs from the circumferential portion: and the former has been named by Rosenthal and Purkinje (xxxiv. 1840, p. 76), the *axis-cylinder;* by Remak

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* Fig. 42. Primitive nerve-tubules. A. A perfectly fresh tubule with a single dark outline. B. A tubule or fibre with a double contour from commencing post-mortem change. C. The changes further advanced producing a varicose or beaded appearance. D. A tubule or fibre, the central part of which, in consequence of still further changes, has accumulated in separate portions within the sheath. After Wagner (cxv).

(xxxviii. June, 1838), the *primitive band*. The outer portion is usually called the medullary or *white substance* of Schwann, being that to which the peculiar white aspect of cerebro-spinal nerves is principally due. The whole contents of the nerve-tubules appear to be extremely soft, for when subjected to pressure they readily pass from one part of the tubular sheath to another, and often cause a bulging at the side of the membrane. They also readily escape, on pressure from the extremities of the tubule, in the form of a grumous or granular material.

That there is an essential difference in chemical composition between the central and circumferential parts of the nerve-fibre, *i.e.*, between the axis-cylinder and the medullary sheath, has of late been clearly shewn by Messrs. Lister and Turner (ccxvii. 1859). Their observations, founded on Mr. Lockhart Clarke's method of investigating nervous substance by means of chromic acid and carmine, have shewn that the axis-cylinder of the nerve-fibre is unaffected by chromic acid, but imbibes carmine with great facility, while the medullary sheath is rendered opaque and brown and laminated by chromic acid, but is entirely untinged by the carmine. From this difference in their chemical behaviour, the central and circumferential portions of the nerve-fibres are readily distinguished on microscopic examination, the former being indicated by a bright-red carmine-coloured point, the latter by a pale ring surrounding it (see also Kölliker, ccxviii. p. 71). The laminated character of the medullary sheath after treatment with chromic acid is believed by Mr. Lockhart Clarke (xliii. 1859) to be due to corrugations effected by the acid, and not to its having a fibrous structure as maintained by Stilling (ccxxii).

The size of the nerve-fibres varies, and the same fibres do not preserve the same diameter through their whole length, being largest in their course within the trunks and branches of the nerves, in which the majority measure from $\frac{1}{2000}$th to $\frac{1}{3000}$th of an inch in diameter. As they approach the brain or spinal cord, and generally also in the tissues in which they

are distributed, they gradually become smaller. In the grey or vesicular substance of the brain or spinal cord, they generally do not measure more than from $\frac{1}{10000}$ to $\frac{1}{14000}$ of an inch (cxiii. Heft. ii.).

The fibres of the second kind, which constitute the principal part of the trunk and branches of the sympathetic nerves, and are mingled in various proportions in the cerebro-spinal nerves, differ from the preceding, chiefly in their fineness, being only about $\frac{1}{2}$ or $\frac{1}{3}$ as large in their course within the trunks and branches of the nerves; in the absence of the double contour; in their contents being apparently uniform; and in their having, when in bundles, a yellowish-grey hue instead of the whiteness of the cerebro-spinal nerves. These peculiarities make it probable that they differ from the other nerve-fibres in not possessing the outer layer of white or medullary nerve-substance; and that their contents are composed exclusively of the substance corresponding with the central portion, or axis-cylinder of the larger fibres. Yet since many nerve-fibres may be found which appear intermediate in character between these two kinds, and since the large fibres, as they approach both their central and their peripheral ends, gradually diminish in size, and assume many of the other characters of the fine fibres of the sympathetic system, it is not necessary to suppose that there must be a material difference in the office or mode of action of the two kinds of fibres.*

Every nerve-fibre in its course proceeds uninterruptedly from its origin at a nervous centre to its destination, whether this be the periphery of the body, in another nervous centre,

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* For the best account of the structure of nerve-fibres, see xxv. 1842, in which is an analysis of the descriptions by Valentin, Henle, Remak, Purkinje, Wagner, Krause, Ehrenberg, and other continental writers; also the notices of more recent investigations, by Will, Hannover, Kölliker, and others, in the subsequent reports; and the various reports in Canstatt's Jahresbericht; see also Dr. Todd and Mr. Bowman in their Physiological Anatomy, and Kölliker in his Manual of Human Microscopic Anatomy, 1860.

or in the same centre whence it issued. In the whole of its course, also, however long, there is no branching or anastomosis or union with the substance of any other fibres.

Bundles, or fasciculi of fibres, run together in the nerves, but merely lie in apposition with each other; they do not unite: even when the fasciculi appear to anastomose there is no union of fibres, but only an interchange of fibres between the anastomosing fasciculi. Hence the central extremity of each fibre is connected with the peripheral extremity of a single nervous fibre only; and this peripheral extremity is in direct relation with only one portion of the brain, spinal cord, or other nervous centre: so that, corresponding to the many millions of primitive fibres which are distributed to peripheral parts of the body, there are the same number of peripheral points of the body represented in the nervous centres. Although each nerve fibre is thus single and undivided through its whole course, yet in the terminal ramifications, individual fibres often break up into several subdivisions, as in the distribution of nerves in striped muscular tissue in the frog, and in other parts.

At certain parts of their course, nerves form *plexuses*, in which they anastomose with each other, and interchange fasciculi, as in the case of the brachial and lumbar plexuses. The object of such interchange of fibres is, probably, to give to each nerve passing off from the plexus, a wider connection with the spinal cord than it would have if it proceeded to its destination without such communication with other nerves. Thus, since the brachial plexus is formed by the intermingling of fasciculi from the four last cervical, and the first dorsal nerves, it is possible that each trunk coming off from it may contain fibres derived from several parts of the cord intermediate between the roots of the fourth cervical and those of the first dorsal. By this means, the parts supplied from the brachial plexus are enabled to have wider relations with the nervous centres, and more extensive sympathies; and, by this means, too, groups of muscles may be associated for combined actions (Gull, lxxxviii. 1849).

The *terminations* of nerve-fibres are their modes of distribution and connection in the nervous centres, and in the parts which they supply: the former are called their *central*, the latter their *peripheral* terminations.

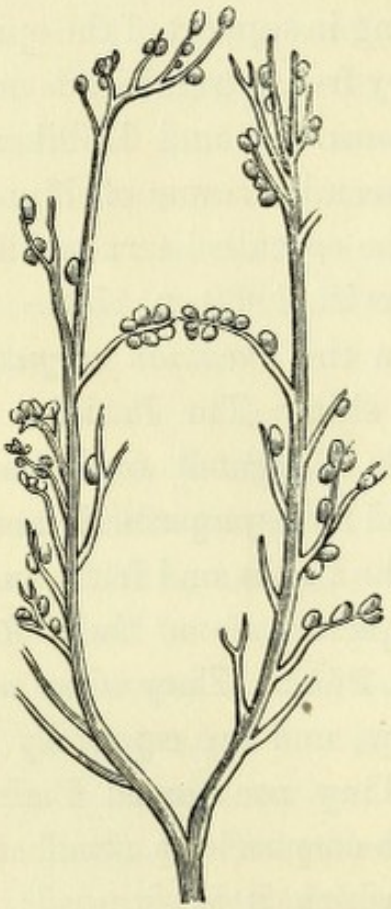
As they approach their final and minutest distribution in the several tissues, the small bundles of nerve-fibres commonly form delicate plexuses, the *terminal plexuses*. These, then dividing or breaking up, give off the primitive fibres, which appear to be disposed of in various ways in different tissues. It is exceedingly difficult to determine how they terminate: but examples of each of the following modes have been observed. 1. In *loops*. In this (which can only conventionally be called a mode of termination); each fibre, after issuing from a branch in a terminal plexus, runs over the elementary structure of the containing tissue, then turns back, and joins the same or a neighbouring branch, in which it probably pursues its way back to a nervous centre. This arrangement has been found in the internal ear (Hannover, cxix.), in the papillæ of the tongue (Todd and Bowman, xxxix. p. 440) and of the skin Kölliker (ccvi. p. 65), in the tooth-pulp (Valentin, xxxix. p. 221), and, in a modified form, in striped muscular tissue (Kölliker, ccvi. p. 184). 2. By *branching*. In the muscular tissue of the frog and the lower Vertebrata, it not unfrequently happens that each ultimate nerve-fibre breaks up into several branches, which spread out over the muscular fibres (Wagner, cxv.; Volkmann, cxxvi. p. 70; Kölliker, ccvi. p. 184). A similar termination by division or branching of the ultimate fibres seems to occur in the retina, and in some other parts. A modification of this mode of termination has been described by Wagner (cxv.) as occurring in the electric organ of the ray. A large nerve-fibre suddenly breaks up into from twelve to fifteen branches, each of which again divides into two secondary branches. Some of these secondary branches anastomose and form a network; while others divide again dichotomously, each of these branches again anastomosing and subdividing, until a very fine network is formed, from which

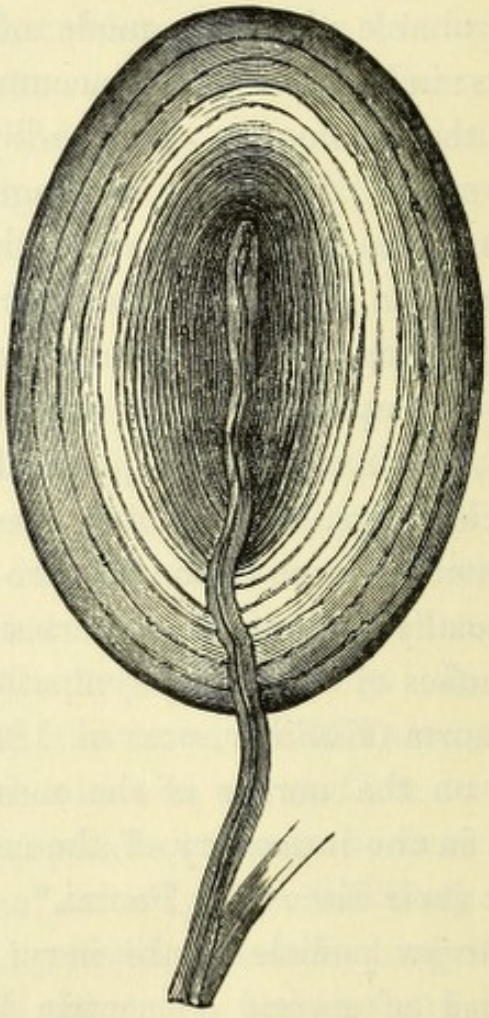
branches pass off, and seem to be lost in the substance of the electric organs. 3. In *plexuses*. Thus, nerve-fibres appear to terminate in certain serous membranes. According to Mr. Rainey (xli. vol. xxix. p. 85), the arachnoid membrane of the brain and spinal cord is traversed by innumerable delicate nerve-fibres, arranged in minute plexuses; and a similar mode of arrangement appears to be observed by the nerve-fibres in other serous membranes, *e.g.*, the peritoneum (Bourgery, xix. 1845; Pappenheim, xviii., 1845). 4. By *free ends*. It is not improbable that this mode of termination exists in several parts: indeed, evidence is accumulating in support of the opinion that the termination of nerve-fibres by free extremities is nearly universal. According to Wagner, Luschke, and Kölliker, its occurrence is well shewn in the muscular tissue of Man and Mammalia, fibres proceeding from the so-called terminal loops and ending in free extremities (ccxviii. 1860, p. 153). The best examples, however, are seen in the *Pacinian corpuscles*, and in some of the papillæ of the skin. The Pacinian corpuscles (figs. 43 and 44) are little elongated oval bodies, situated on some of the cerebro-spinal and sympathetic nerves, especially the cutaneous nerves of the hands and feet: and on branches of the large sympathetic plexus about the abdominal aorta (Kölliker, ccxviii. 1860, p. 248). They often occur also on the nerves of the mesentery, and are especially well seen in the mesentery of the cat. They are named Pacinian after their discoverer Pacini.* Each corpuscle is attached by a narrow pedicle to the nerve on which it is situated; it is formed of several concentric layers of fine membrane, with intervening spaces centaining fluid; through its pedicle passes a single nerve-fibre, which, after traversing the several concentric layers and their intermediate spaces, enters a central cavity, and gradually losing its dark border, and becoming

* See for a description of these bodies an abstract of Henle and Kölliker's essay on them (xxv. 1843—4, p. 46); Mr. Bowman in the Cyclopædia of Anatomy and Physiology; Kölliker (ccvi. and ccxviii.) and Huxley (ccxvii. vol. i.).

smaller, terminates at or near the distal end of the cavity, in a knob-like enlargement, or in a bifurcation. The enlargement commonly found at the end of the fibre, is said by Pacini (cxx. 1845, p. 208) to resemble a ganglion corpuscle; but this observation has not been confirmed. The physiological import of these bodies seems to be still quite obscure. In some of the tactile papillæ of the skin, nerve-fibres terminate

*Fig.* 43.* *Fig.* 44.†





in a small oval body, not unlike, in form and structure, the Pacinian corpuscles: they will be described when speaking of the sense of touch. 5. Lastly, the fibres sometimes terminate

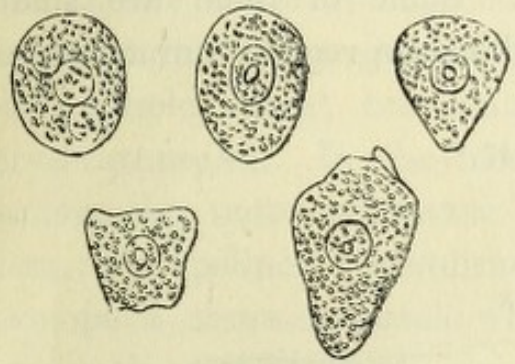
* Fig. 43. Extremities of a nerve of the finger with Pacinian corpuscles attached, about the natural size. Adapted from Henle and Kölliker.

† Fig. 44. A magnified view of a single Pacinian corpuscle, shewing its laminated structure, and the termination of the nerve-fibre in its central cavity. After Bendz (lxxix.).

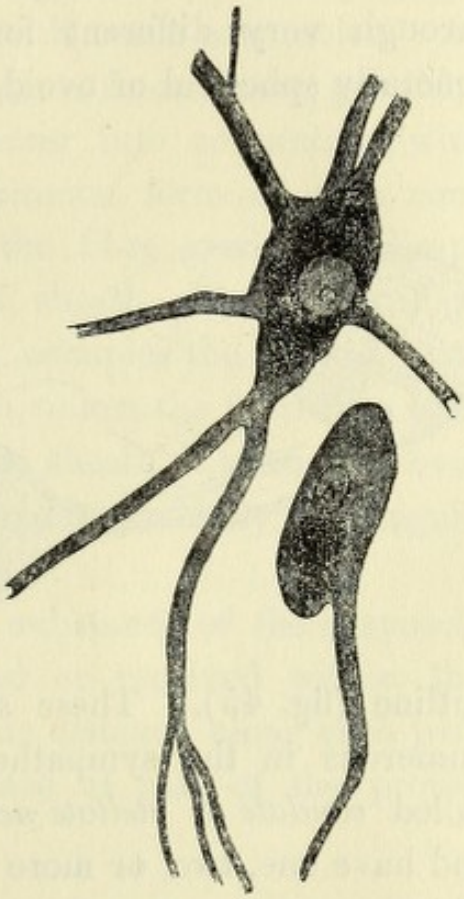
in *nerve-corpuscles*. This has been determined to be the case in the retina and in the lamina spiralis of the internal ear, and probably is so in other parts.

The *central* termination of nerve-fibres can be better considered after the account of the vesicular nerve-substance.

* *Fig.* 45.



† *Fig.* 46.



The *vesicular* nervous substance is composed, as its name implies, of vesicles or corpuscles, which are commonly called nerve-corpuscles, or ganglion-corpuscles. These are found chiefly in the nervous centres, *i. e*, the brain, spinal cord, and the various ganglia, but occasionally also in the nervous trunks; they are mingled with nerve-fibres, and imbedded in a dimly-shaded or granular substance; they give to the ganglia and to certain parts of the brain and spinal cord

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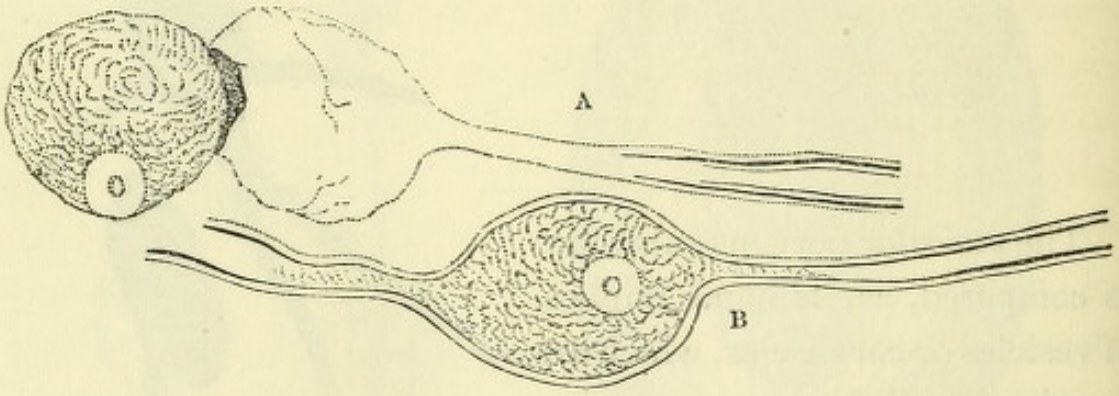
* Fig. 45. Nerve-corpuscles from a ganglion; after Valentin. In one a second nucleus is visible. In several the nucleus contains one or two nucleoli.

† Fig. 46. Stellate or caudate nerve-corpuscles, with tubular processes issuing from them. Besides being filled with granular material continuous with the contents of the processes, the corpuscles contain black pigment-matter. After Hannover (cxix.).

the peculiar greyish or reddish-grey aspect by which these parts are characterized. They are large nucleated cells, filled with a finely granular material, some of which is often dark like pigment: the nucleus, which is vesicular, contains a nucleolus (fig. 45). Besides varying much in shape, partly in consequence of mutual pressure, they present such other varieties as make it probable either that there are two different kinds, or that in the stages of their development, they pass through very different forms. Some of them are small, generally spherical or ovoid, and have a regular uninterrupted

*Fig.* 47.*




outline (fig. 45). These *simple* nerve-corpuscles are most numerous in the sympathetic ganglia. Others, which are called *caudate* or *stellate nerve-corpuscles* (fig. 46), are larger, and have one, two, or more long processes issuing from them, which processes often divide and subdivide, and appear tubular, and filled with the same kind of granular material as is

* Fig. 47. Connection between nerve-fibres and nerve-corpuscles; from the roots of a spinal nerve of the Ray. After Wagner (CXV.). A. A nerve-corpuscle, escaped by pressure from the capsule formed around it by the dilated sheath of the nerve-tubule: it shows also the gradual disappearance of the outer portion of the substance of the nerve as it comes into relation with the corpuscles. B. A nerve-corpuscle enclosed within a dilated portion of the sheath of a nerve: part of the granular material of the corpuscle is continuous with the central substance of the nerve in the course of which it is inserted.

contained within the corpuscle. Of these processes some appear to taper to a point, and terminate at a greater or less distance from the corpuscle; others may be traced until each of them, gradually losing its granular appearance, becomes continuous with, and acquires all the characters of, a perfect nerve-fibre (fig. 47).

It is probable that many nerve-fibres, when they enter a nervous centre, terminate, or perhaps, more correctly, originate in this mode of connection with nerve-corpuscles. As they enter, the fibres gradually become finer: some, possibly, form simple loops; but many enter into connection with nerve-corpuscles. In the most common form of such connection, the outer substance of the fibre gradually disappears, the pellucid membranous sheath dilates, as if to envelope a nerve-corpuscle which occupies the dilated part; the sheath again contracts, and then, unless the fibre thus ends in the corpuscle (as at A. fig. 47), its sheath is continued over to the other side of the corpuscle, and is gradually filled again with its proper substance (fig. 47, B).

A prolongation of the granular substance of the corpuscle which thus appears to be inserted or received within the sheath of the fibre, extends for some distance along each part of the nerve-tube, taking the place of part of the proper substance of the fibre.*

### *Functions of Nerve-Fibres.*

The office of the nerves as simple conveyers or conductors

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* On this origin of nerve-fibres in ganglia, consult Bidder and Volkmann (cxxvi.); and for nearly all that has been written on the connection of nerve-fibres with ganglion-corpuscles, see, in addition to Bidder's account, Wagner (cxv. and xv. art. *Sympathischer Nerven*); Hannover (cxix.); Todd and Bowman (xxxix.); Kölliker (cxiv. ccxii. and ccxviii.); and for a summary of the observations of these and other physiologists refer to Henle's report in Canstatt's Jahresbericht for 1847, p. 58, and the subsequent reports to 1859.

of nervous impressions is of a two-fold kind. First, they serve to convey to the nervous centres the impressions made upon their peripheral extremities, or parts of their course; and in this way the mind, through the medium of the brain, may become conscious of external objects. Secondly, they serve to transmit impressions from the brain and other nervous centres to the parts to which the nerves are distributed; and these impressions seem to be of at least two kinds, those, namely, which excite muscular contractions, and those which influence the secretion, nutrition, and other organic functions of a part.

For this twofold office of the nerves two distinct sets of nerve-fibres are provided, in both the cerebro-spinal and sympathetic systems. Those which convey impressions from the periphery to the centre are classed together as *centripetal* or *afferent* nerves, or, when speaking exclusively of cerebro-spinal nerves, *nerves of sensation*, or *sensitive nerves*. Those fibres, on the other hand, which are employed to transmit central impulses to the muscles are classed as *centrifugal*, *efferent*, or *motor* nerves, or *nerves of motion*. The nervous influence by which secretion and nutrition are controlled seems to be conveyed (as already stated, pp. 306—329) along both sensitive and the centrifugal sympathetic nerves.

With this difference in the functions of nerves, there is no apparent difference in the structure of the nerve-fibres by which it might be explained. Among the cerebro-spinal nerves, the fibres of the olfactory, optic, and auditory nerves are finer than those of the nerves of common sensation, and more like the fibres in the brain: but with these exceptions no centripetal fibres can be distinguished in their microscopic or general characters from those of motor nerves. Neither can the difference in function be due to the kind of tissue to which a nerve is distributed; for although the nerves supplying muscles are principally motor, yet the muscular tissue contains sensitive fibres also, for pain is felt when it is injured, and, as will be hereafter shewn, much of the exactness and

precision of muscular action is determined by the power which the muscular tissue has of communicating to the mind the sensation of its own contraction, and of the effects produced by it.

Nerve-fibres appear to possess no power of generating force in themselves, or of originating impulses to action: for the manifestation of their peculiar endowments they require to be stimulated. They possess a certain property of conducting impressions, a property which has been named excitability; but this is never manifested till some *stimulus* is applied (see pp. 32, 33). Under ordinary circumstances nerves of sensation are stimulated by external objects acting upon their extremities; and the nerves of motion by the will, or by some force generated in the nervous centres. But almost all things that can disturb the nerves from their passive state act as stimuli, and agents the most dissimilar produce the same kind, though not the same degree of effect, because that on which they act possesses but one kind of excitable force. Thus all stimuli, as well the internal organic as the inorganic,—the chemical, mechanical, and electric,—when applied to parts endowed with sensation, or to sensitive nerves (the connection of the latter with the brain and spinal cord being uninjured) produce sensations; and when applied to the nerves of muscles excite contractions. Muscular contraction is produced as well when the motor nerve is still in connection with the brain, as when its communication with the nervous centres is cut off by dividing it; nerves, therefore, have, by virtue of their excitability, the property of exciting contractions in muscles to which they are distributed; and the part of the divided motor nerve which is connected with the muscle, will still retain this power, however much we may curtail it; but irritation of the other portion, which is in connection with the brain, never excites contractions of the muscles.

Mechanical irritation, when so violent as to injure the texture of the primitive nerve-fibres, deprives the centripetal nerves of their power of producing sensations when irritation

is again applied at a point more distant from the brain than the injured spot; and in the same way, no irritation of a motor nerve will excite contraction of the muscle to which it is distributed, if the nerve has been compressed and bruised between the point of irritation and the muscle; the effect of such an injury being the same as that of division.

The action of nerves is also excited by *temperature*. Thus, when heat is applied to the nerve going to a muscle, or to the muscle itself, contractions are produced. These contractions are very violent when the flame of a candle is applied to the nerve, while less elevated degrees of heat,—for example, that of a piece of iron merely warmed,—do not irritate sufficiently to excite action of the muscles. The application of cold has the same effect as that of heat. The effect of the local action of excessive or long-continued cold or heat on the nerves, is the same as that of destructive mechanical irritation. The sensitive and motor power in the part is destroyed, but the other parts of the nerve retain their excitability; and, after the extremity of a divided nerve going to a muscle has been burnt, contractions of the muscle may be excited by irritating the nerve below the burnt part.

*Chemical Stimuli* excite the action of both sensitive and motor nerves as mechanical irritants do; provided their effect is not so strong as to destroy the structure of the nerve to which they are applied. A like manifestation of nervous power is produced by *electricity* and by *magnetism*.

Some of these laws regulating the excitability of nerves, and their power of manifesting their functions, require further notice, with several others which have not yet been alluded to. Certain of the laws and conditions of actions relate to nerves both of sensation and motion, being dependent on properties common to all nerve-fibres; while of others, some are peculiar to nerves of motion, some to nerves of sensation.

It is a law of action in all nerve-fibres, and corresponds with the continuity and and simplicity of their course, that an

impression made on any fibre, is simply and uninterruptedly transmitted along it, without being imparted or diffused to any of the fibres lying near it. In other words, all nerve-fibres are mere *conductors* of impressions. Their adaptation to this purpose is, perhaps, due to the contents of each fibre being completely isolated from those of adjacent fibres by the membrane or sheath in which each is enclosed, and which acts, it may be supposed, just as silk, or other non-conductors of electricity, when covering a wire, prevent the electric condition of the wire from being conducted into the surrounding medium.

Nervous force travels along nerve-fibres with an immeasurable velocity. A certain period of time probably does elapse in the transit of an impression from one end of a fibre to the other; but its length is inappreciable, and will probably never be ascertained, while we have not the opportunity of tracing the passage through distances as vast as those through which the passage of light is calculated. (See, however, Helmholtz, lxxi. vol. x. n. s. p. 472). It has been supposed, indeed, that the velocity is less in some persons than in others; chiefly because the impression of an object on the retina is sometimes perceived rather later by one person than by another—the difference amounting to one-third, or one-half, or even a whole second. The cases in which this difference has been chiefly observed, are those in which the two senses of sight and hearing are simultaneously engaged in noting the exact moment at which a star passes before the thread crossing the field of a telescope. While the constant motion of the star across the field is followed with the eye, the ear notes each stroke of the pendulum-clock which stands near, marking the seconds. Now, it frequently happens, when two persons are thus engaged in making the same observation, that one of them notes the transit of the star later than the other; as if either the velocity with which the impression of the star passes along the optic nerve, were less in one than in the other; or, as if one nerve conveyed impressions more rapidly than another, so that

the one person would see before he hears, the other hear before seeing. But, a more probable explanation is, that both impressions are conveyed with the same immeasurable velocity, but the mind does not at the same instant take cognizance of both—for the mind does not readily perceive with equal distinctness two different simultaneous impressions, but rather, when several impressions are made on the nerves at the same time, takes cognizance of only one at a time, and perceives the rest in succession. When, therefore, both hearing and sight are directed simultaneously to different objects, the mind may first hear and then see, and the interval of time between the two perceptions may be greater in some persons than in others; or some persons may be conscious at the same moment of many impressions, between which others require a considerable interval.

No nerve-fibre can convey more than one kind of impression. Thus, a motor fibre can convey only motor impulses, that is, such as may produce movements in contractile parts: a sensitive fibre can transmit none but such as may produce sensation, if they are propagated to the brain. Moreover, the fibres of a nerve of special sense, as the optic or auditory, can convey only such impressions as may produce a peculiar sensation, *e. g.*, that of light or sound. While the rays of light, and the sonorous vibrations of the air, are without influence on the nerves of common sensation, the other stimuli, which may produce pain when applied to them, produce, when applied to these nerves of special sense, only morbid sensations of light, or sound, or taste, according to the nerve impressed.

Of the laws of action peculiar to nerves of sensation and of motion respectively, many can be ascertained only by experiments on the roots of the nerves. For it is only at their origin that the nerves of sensation and of motion are distinct; their filaments, shortly after their departure from the nervous centres, are mingled together, so that nearly all nerves, except those of the special senses, consist of both sensitive and motor filaments, and are hence termed mixed nerves.

Among the laws of action of *nerves of sensation* is, 1st, that these nerves appear able to convey impressions only from the parts in which they are distributed, towards the nervous centre from which they arise, or to which they tend. Thus, when a sensitive nerve is divided, and irritation is applied to the end of the proximal portion, *i. e.*, of the portion still connected with the nervous centre, sensation is perceived, or a reflex action ensues; but, when the end of the distal portion of the divided nerve is irritated, no effect appears. The absence of effect in the latter case is, perhaps, not to be ascribed to the distal portion of the nerve being completely cut off from connection with the nervous centre, for it may contain fibres which, after reaching their destination, return through loops back to a nervous centre; rather, it may be believed, that the sensitive fibres cannot convey impressions in any direction except towards the nervous centres.

When an impression is made upon any part of the course of a sensitive nerve, the mind may perceive it as if it were made not only upon the point to which the stimulus is applied, but also upon all the points in which the fibres of the irritated nerve are distributed: in other words, the effect is the same as if the irritation were applied to the parts supplied by the branches of the nerve. When the whole trunk of the nerve is irritated, the sensation is felt at all the parts which receive branches from it: but when only individual portions of the trunk are irritated, the sensation is perceived at those parts only which are supplied by the several portions. Thus, if we compress the ulnar nerve where it lies at the inner side of the elbow-joint, behind the internal condyle, we have the sensation of "pins and needles," or of a shock, in the parts to which its fibres are distributed; namely, in the palm and back of the hand, and in the fifth and ulnar half of the fourth finger. When stronger pressure is made, the sensations are felt in the fore-arm also; and, if the mode and direction of the pressure be varied, the sensation is felt by turns in the fourth finger, in the fifth, in the palm of the hand, or in the back of the hand,

according as different fibres or fasciculi of fibres are more pressed upon than others.

It is in accordance with this law, that when parts are deprived of sensibility by compression or division of the nerve supplying them, irritation of the portion of the nerve connected with the brain still excites sensations which are felt as if derived from the parts to which the peripheral extremities of the nerve-fibres are distributed. Thus, there are cases of paralysis in which the limbs are totally insensible to external stimuli, yet are the seat of most violent pain, resulting apparently from irritation of the sound part of the trunk of the nerve still in connection which the brain, or from irritation of those parts of the nervous centre from which the sensitive nerve or nerves supplying the paralysed limbs originate.

An illustration of the same law is also afforded by the cases in which division of a nerve for the cure of neuralgic pain is useless, and in which the pain continues or returns, though portions of the nerve be removed. In such cases, the disease is probably seated nearer the nervous centre than the part at which the division of the nerve is made, or it may be in the nervous centre itself. When the cause of the neuralgia is seated in the trunk of the nerve—for example, of the facial or infra-orbital nerve—division of the branches can be of no service ; for the stump remaining in connection with the brain and containing all the fibres distributed in the branches of the nerve to the skin, continues to give rise, when irritated, to the same sensations as are felt when the peripheral parts themselves are affected. Division of a nerve prevents the possibility of external impressions on the cutaneous extremities of its fibres being felt; for these impressions can no longer be communicated to the brain: but the same sensations which were before produced by external impressions may arise from internal causes. In the same way may be explained the fact, that when part of a limb has been removed by amputation, the remaining portions of the nerves which ramified in it may give rise to sensations which the mind refers to the lost part.

When the stump and the divided nerves are inflamed, or pressed, the patient complains of pain felt as if in the part which has been removed. When the stump is healed, the sensations which we are accustomed to have in a sound limb are still felt; and tingling and pains are referred to the parts that are lost, or to particular portions of them, as to single toes, to the sole of the feet, to the dorsum of the foot, etc.

But (as Volkmann shews) it must not be assumed, as it often has been, from these examples, that the mind has no power of discriminating the very point in the length of any nerve-fibre to which an irritation is applied. Even in the instances referred to, the mind perceives the pressure of a nerve at the point of pressure, as well as in the seeming sensations derived from the extremities of the fibres: and in stumps, pain is felt in the stump, as well as, seemingly, in the parts removed. In the natural state of parts, also, the mind discerns the very part of a nerve-fibre that is irritated. Thus, if a needle's point be drawn in a straight line across the back, or the thigh, or any part in which nerve-fibres are widely placed, the mind perceives the line of irritation as a straight one; whereas, if it referred all impressions to the ends of irritated fibres, this mode of irritation should be felt in sensations variously scattered about the line, in the points at which the nerve-fibres crossed by the needle terminate. So, in the case of the retina, it is certain that its whole inner surface is not so covered with the ends of nerve-fibres, as that the images of any two points or lines which appear distinct must always fall on different fibres; but if, in any case, the two images fall on different parts of the same fibres, and the mind perceives them as distinct objects, it must be because the mind can discern the very point or points of a nerve-fibre on which an impression falls.

The conclusions from both these sets of facts may be, that in the natural state of the parts, and on the application of ordinary stimuli, the mind can so distinctly discern an impres-

sion made on any point in the length of a nerve-fibre as to refer it to that point; and even when, as in the case of impressions on the retina, two or more are made at the same instant on different points of the same fibre, it can discriminate and perceive them both as distinct and as proceeding from definitely related objects; but that in morbid states of the nerves, and, in the case of unusual stimuli, the impressions made on nerve-fibres in their course are referred by the mind rather to parts from which it is in the habit of receiving impressions through those nerves, than to the parts of the nerve-fibres on which the stimulus or irritation is applied.

The habit of the mind to refer impressions received through the sensitive nerves to the parts from which impressions through those nerves are, or were, commonly received, is further exemplified when the relative position of the peripheral extremities of sensitive nerves is changed artificially, as in the transposition of portions of skin. When, in the restoration of a nose, a flap of skin is turned down from the forehead and made to unite with the stump of the nose, the new nose thus formed has, as long as the isthmus of skin by which it maintains its original connections remains undivided, the same sensations as if it were still on the forehead; in other words, when the nose is touched, the patient feels the impression as if it were derived from the forehead. When the communication of the nervous fibres of the new nose with those of the forehead is cut off by division of the isthmus of skin, the sensations are no longer referred to the forehead; the sensibility of the nose is at first absent, but is gradually developed.

When, in a part of the body which receives two sensitive nerves, one is paralysed, the other is inadequate to maintain the sensibility of the entire part; the extent to which the sensibility is preserved corresponds with the number of the fibres unaffected by the paralysis. This is a consequence of the isolation and simplicity of the several nerve-fibres, so that, as already observed, even when nerves appear to anastomose, their several fibres continue separate and distinct, as isolated con-

ductors of impressions. Thus, when the ulnar nerve, which supplies the fifth and a part of the fourth finger, is divided, the sensibility of those parts is not supplied through the medium of the branches which the ulnar derives from the median nerve; but the fourth and fifth fingers are permanently deprived of sensibility.

Several of the laws of action in *motor nerves* correspond with the foregoing. Thus, the motor influence is propagated only in the direction of the fibres going to the muscles; by irritation of a motor nerve, contractions are excited in all the muscles supplied by the branches given off by the nerve below the point irritated, and in those muscles alone: the muscles supplied by the branches which come off from the nerve at a higher point than that irritated, are never directly excited to contractions. No contraction, for instance, is produced in the frontal muscle by irritating the branches of the facial nerve that ramify upon the face; because that muscle derives its motor nerves from the trunk of the facial previous to these branches. So, again, because the isolation of motor nerve-fibres is as complete as that of sensitive ones, the irritation of a part of the fibres of a motor nerve does not affect the motor power of the whole trunk, but only that of the portion to which the stimulus is applied. And it is because of the same fact that when a motor nerve enters a plexus, and contributes with other nerves to the formation of a nervous trunk proceeding from the plexus, it does not impart motor power to the whole of that trunk, but only retains it isolated in the fibres which form its continuation in the branches of that trunk.

### *Functions of Nervous Centres.*

As already observed (p. 377), the term "nervous centre" is applied to all those parts of the nervous system which contain ganglion-corpuscles, or vesicular nerve-substance, *i. e.*, the

brain, spinal cord, and the several ganglia which belong to the cerebro-spinal and the sympathetic systems. Each of these nervous centres has a proper range of functions, the extent of which bears a direct proportion to the number of nerve-fibres that connect it with the various organs of the body, and with other nervous centres; but they all have certain general properties and modes of action common to them as nervous centres.

It is generally regarded as the property of nervous centres, that they originate the impulses by which muscles may be excited to action, and by which the several functions of organic life may be maintained. Hence, they are often called *sources* or *originators* of nervous power or force. But, the instances in which these expressions can be strictly used are few. It is possible that the ganglia of the heart are the spontaneous sources of the nervous force that excites its rhythmical contractions; that the medulla oblongata may originate the force exciting the co-ordinate and adapted acts of the first respirations; and that from the spinal cord is derived the force under which the sphincter ani is held in uniform contraction; but with these exceptions (if they are such) few or no motor impulses proceed spontaneously from the nervous centres.* The brain does not issue any except when itself impressed by the will, or stimulated by an impression from without; neither without such previous impressions do the other nervous centres produce or issue motor impulses. The intestinal ganglia, for example, do not give out the nervous force necessary to the contractions of the intestines except when they receive, through their centripetal nerves, the stimuli of substances in the intestinal canal. So also, the spinal cord; for a decapitated animal lies motionless so long as no irritation is applied to its

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* The case of that modification of *tone* which consists in a permanent, and seemingly passive, slight contraction of the muscles, is not here in view.

centripetal nerves, though the moment they are touched movements ensue.

The more certain and general office of all the nervous centres is that of variously disposing and transferring the impressions that reach them through their several centripetal nerve-fibres. In nerve-fibres, as already said, impressions are only *conducted* in the simple isolated course of the fibre; in all the nervous centres an impression may be not only conducted, but also communicated: in the brain alone it may be *perceived* (see p. 34).

*Conduction in or through nervous centres* may be thus simply illustrated. The food in a given portion of the intestines, acting as a stimulus, produces a certain impression on the nerves in the mucous membrane, which impression is conveyed through them to the adjacent ganglia of the sympathetic. In ordinary cases, the consequences of such an impression on the ganglia is the movement of the muscular coat of that and the near adjacent portions of the canal. But, if irritant substances be mingled with the food, the sharper stimulus produces a stronger impression, and this is *conducted through* the nearest ganglia to others more and more distant; and, from all these, motor impulses issuing, excite a wide-extended and more forcible action of the intestines. Or, even through all the sympathetic ganglia, the impression may be further conducted to the ganglia of the spinal nerves, and through them to the spinal cord, whence may issue motor impulses to the abdominal and other muscles, producing cramp. And yet further, the same morbid impression may be conducted through the spinal cord to the brain, where the mind may perceive it. In the opposite direction, mental influence may be conducted from the brain through a succession of nervous centres—the spinal cord and ganglia, and one or more ganglia of the sympathetic —to produce the influence of the mind on the digestive and other organic functions. In short, in all cases in which the mind either has cognizance of, or exercises influence on, the processes carried on in any part supplied with sympathetic

nerves, there must be a *conduction* of impressions through all the nervous centres between the brain and that part. It is probable that in this conduction through nervous centres the impression is not propagated through uninterrupted nerve-fibres, but is conveyed through successive nerve-vesicles and connecting nerve-filaments. In some instances, and when the stimulus is exceedingly powerful, the conduction may be effected as quickly as through continuous nerve-fibres; but with less stimulus it may occupy some minutes in its transit. Thus, *e.g.*, in stimulating the semilunar ganglia of the stomach, movements slowly ensue in the stomach; on touching the heart, all its fibres very soon contract, yet not in that instantaneous manner in which the fibres of a voluntary muscle contract when its nervous trunk is irritated.

But instead of, or as well as, being conducted, impressions made on nervous centres may be *communicated* from the fibres that brought them, to others; and in this communication may be either *transferred*, *diffused*, or *reflected*.

The *transference of impressions* may be illustrated by the pain in the knee, which is a common sign of disease of the hip. Here the impression made by the disease on the nerves of the hip-joint, is conveyed to the spinal cord; there it is *transferred* to the central ends or connections of the nerve-fibres of the knee-joint. Through these the transferred impression is conducted to the brain, and the mind, referring the sensation to the part from which it usually through these fibres receives impressions, feels as if the disease and the source of pain were in the knee. At the same time that it is transferred, the primary impression may be also conducted; and in this case, pain is felt in both the hip and the knee. So, not unfrequently, if one touches a small pimple that may be seated in the trunk, a pain will be felt in as small a spot on the arm, or some other part of the trunk. And so, in whatever part of the respiratory organs an irritation may be seated, the impression it produces is transferred to the nerves of the larynx; and then the mind perceives the peculiar sensation of tickling

in the glottis, which best, or almost alone, excites the act of coughing. Or, again, when the sun's light falls strongly on the eye, a tickling may be felt in the nose, exciting sneezing. In all these cases, the primary impression may be conducted as well as transferred; and in all it is transferred to a certain set of nerves which generally appear to be in some purposive relation with the nerves first impressed.

The *diffusion* or *radiation of impressions* is shown when an impression received at a nervous centre is diffused to many other fibres in the same centre, and produces sensations extending far beyond, or in an indefinite area around, the part from which the primary impression was derived. Hence, as in the former cases, result various kinds of what have been denominated sympathetic sensations. Sometimes such sensations are referred to almost every part of the body; as in the shock and tingling of the skin produced by some startling noise. Sometimes only the parts immediately surrounding the point first irritated participate in the effects of the irritation; thus, the aching of a tooth may be accompanied by pain in the adjoining teeth, and in all the surrounding parts of the face; the explanation of such a case being, that the irritation conveyed to the brain by the nerve-fibres of the diseased tooth is *radiated* to the central ends of adjoining fibres, and that the mind perceives this secondary impression as if it were derived from the peripheral ends of the fibres. Thus, also, the pain of a calculus in the ureter is diffused far and wide.

All the preceding examples represent impressions communicated from one sensitive fibre to others of the same kind; or from fibres of special sense to those of common sensation. A similar communication of impressions from sensitive to motor fibres, constitutes *reflection of impressions*, displays the important functions common to all nervous centres as *reflectors*, and produces *reflex movements*. In the extent and direction of

such communications, also, phenomena corresponding to those of transference and diffusion to sensitive nerves, are observed in the phenomena of reflection. For, as in transference, the reflection may take place from a certain limited set of sensitive nerves to a corresponding and related set of motor nerves; as when in consequence of the impression of light on the retina, the iris contracts, but no other muscle moves. Or, as in diffusion or radiation, the reflection may bring widely-extended muscles into action; as when an irritation in the larynx brings all the muscles engaged in expiration into coincident movement.

It will be necessary, hereafter, to consider in detail so many of the instances of the reflecting power of the several nervous centres, that it may be sufficient here to mention only the most general rules of reflex action.

1. For the manifestation of every reflex action, three things are necessary; first, one or more perfect centripetal nerve-fibres, to convey an impression; 2ndly, a nervous centre to which this impression may be reflected, and by which it may be reflected; 3rdly, one or more centrifugal nerve-fibres, upon which this impression may be reflected, and by which it may be conducted to the contracting tissue. In the absence of either of these three conditions, a proper reflex movement could not take place; and whenever impressions made by external stimuli on sensitive nerves give rise to motions, these are never the result of the direct reaction of the sensitive and motor fibres of the nerves on each other; in all such cases, the impression is conveyed by the sensitive fibres to a nervous centre, and is therein communicated to the motor fibres.

2. All reflex actions are essentially involuntary; all may be accomplished independent of the will, though most of them admit of being modified, controlled, or prevented by a voluntary effort. All are perfectly performed without education or previous experience, although some, as coughing and the like, are not well performed unless the will have previously made some preparatory movement.

3. All reflex actions performed in health, have a distinct purpose, and are adapted to secure some end desirable for the well-being of the body; but, in disease, many of them are irregular and purposeless. As an illustration of the first point may be mentioned movements of the digestive canal, the respiratory movements, the contraction of the eyelids and the pupil to exclude many rays of light, when the retina is exposed to a bright glare. These and all other normal reflex acts afford, also, examples of the mode in which the nervous centres *combine* and arrange co-ordinately the actions of the nerve-fibres, so that many muscles may act together for the common end. Another instance of the same kind is furnished by the spasmodic contractions of the glottis on the contact of carbonic acid, or any foreign substance, with the internal surface of the epiglottis or larynx. Examples of the purposeless irregular nature of morbid reflex actions are seen in the convulsive movements of epilepsy, and in the spasms of tetanus and hydrophobia.

4. Reflex muscular acts are commonly more sustained than those produced by the direct stimulus of muscular nerves. As Volkmann relates (lxxx. 1845), the irritation of a muscular organ, or its motor nerve, produces contraction lasting only so long as the irritation continues; but irritation applied to a nervous centre through one of its centripetal nerves, excites reflex and harmonious contractions, which last some time after the withdrawal of the stimulus.

## CEREBRO-SPINAL NERVOUS SYSTEM.

The physiology of the cerebro-spinal nervous system includes that of the spinal cord, medulla oblongata and brain, of the several nerves given off from each, and of the ganglia on those nerves. It will be convenient to speak first of the spinal cord and its nerves.

### *Spinal Cord and its Nerves.*

The spinal cord is a cylindriform column of nerve-substance, connected above with the brain through the medium of the medulla oblongata, terminating below, about the first or second lumbar vertebra, in a slender filament of grey or vesicular substance, the *filum terminale*, which lies in the midst of the roots of many nerves forming the *cauda equina*. The cord is composed of fibrous and vesicular nervous substance, of which the former is situated externally, and constitutes its chief portion, while the latter occupies its central or axial portion, and is so arranged, that on the surface of a transverse section of the cord it appears like two somewhat crescentic masses connected together by a narrower portion or isthmus.

The spinal cord consists of two exactly symmetrical halves united in the middle line by a *commissure*, but separated anteriorly and posteriorly by a vertical *fissure;* the posterior fissure being deeper, but less wide and distinct than the anterior. Each half of the spinal cord is marked on the sides (obscurely at the lower part, but distinctly above,) by two longitudinal furrows, which divide it into three portions, columns, or tracts, an *anterior*, *middle* or *lateral*, and *posterior*. From the groove between the anterior and lateral columns spring the *anterior roots* of the spinal nerves; and just in front of the groove between the lateral and posterior column arise the *posterior roots* of the same: a pair of roots on each side corresponding to each vertebra.

The fibrous part of the cord contains continuations of the innumerable fibres of the spinal nerves issuing from it, or entering it; but is, probably, not formed of them exclusively; nor a mere trunk, like a great nerve, through which they may pass to the brain. It is, indeed, among the most difficult things in structural anatomy to determine the course of individual nerve-fibres, or even of fasciculi of fibres, through even a short distance of the spinal cord: and it is only by the

examination of transverse and longitudinal sections through the substance of the cord, such as those so successfully made by Mr. Lockhart Clarke (xliii. 1851 to 1859), that we can obtain anything like a correct idea of the direction taken by the fibres of the roots of the spinal nerves within the cord. From the information afforded by such sections it would appear, that of the root-fibres of the nerves which enter the cord, some assume a transverse, others a longitudinal direction: the fibres of the former pass horizontally or obliquely into the substance of the cord, in which many of them appear to become continuous with fibres entering the cord from other roots, others pass into the columns of the cord, while some, perhaps, terminate at or near the part which they enter: of the fibres of the second set, which usually first traverse a portion of the grey substance, some pass upwards, and others, at least of the posterior roots, turn downwards, but how far they proceed in either direction, or in what manner they terminate, are questions still undetermined. It is probable, that of these latter, many constitute longitudinal commissures, connecting different segments of the cord with each other, while others, probably, pass directly to the brain. That all do not pass to the brain, is rendered probable by many circumstances. First, if they did so, the thickness of the spinal cord ought to increase from below upwards, in the same proportion as fresh fasciculi of fibres are added to it by each pair of spinal nerves; and the portion nearest the medulla oblongata ought to be thicker than any part below it. But this is certainly not the case: the upper part of the cervical portion of the cord is smaller than the lower part; and both it and the middle of the dorsal portion are smaller than the lumbar portion. The general rule respecting the size of different parts of the cord appears to be, that the size of each part bears a direct proportion to the size and number of nerve-roots given off from itself, and has but little relation to the size or number of those given off below it. Thus, the cord is very large in the middle and lower part of its cervical portion, whence arise the large nerve-

roots for the formation of the brachial plexuses and the supply of the upper extremities, and again enlarges at the lowest part of its dorsal portion and the upper part of its lumbar, at the origins of the large nerves which, after forming the lumbar and sacral plexuses, are distributed to the lower extremities. Together with this increase of the white substance, there is, however, a corresponding increase in the quantity of grey matter to which the greater thickness of the cord, at such parts, is also in some measure due.

That such enlargements, occurring at parts of the cord which give off nerves of unusual size, are due to actual increase of nervous substance, has been proved by Volkmann (xv. art. *Nervenphysiologie*). He weighed four pieces of a horse's spinal cord, each seven centimetres long, and taken respectively from below the second, the eighth, the nineteenth, and the thirtieth pairs of nerves, and found that their weights, in this order, were 219, 293, 163, and 281 grains. On measurement, he found that the areas of the transverse sections of the grey matter in them were (in the same order) 13, 28, 11, and 25 square lines; and those of the white matter 109, 142, 89, and 121 square lines. It thus appeared, that the quantity of white or fibrous substance of the cord is absolutely less at the cervical than at the lowest part of the lumbar portion; which it could not be, if the cord, in its progress from below upwards, retained any quantity of the fibres successively received from the roots of the spinal nerves. On the other hand, the enlargement and increased weight of the cord at parts exactly corresponding to the origin of the larger and most numerous nerves, and its diminution immediately above and below such parts, make it most probable that the fibres composing the roots of those nerves arise directly from the largest parts of the cord, and not from any parts higher up.

Although, however, this statement by Volkmann may be in great measure true for the horse and other animals, yet the observations of Kölliker and others make it probable that, in the case of man, the white or fibrous substance of the cord does

regularly and progressively increase from below upwards, in consequence, no doubt, of the continual addition of fresh fasciculi from each pair of nerves; and that, therefore, as already said, many of the fibres proceed through the cord in simple and uninterrupted continuity to the brain.

It may be added, however, that there is no sufficient evidence for the supposition, that an uninterrupted continuity of nerve-fibres is essential to the conduction of impressions on the spinal nerves to and from the brain: such impressions may be as well transmitted through the nerve-vesicles of the cord as by the nerve-fibres; and the experiments of Brown-Séquard, again to be alluded to, make it probable that the grey substance of the cord is the only channel through which sensitive impressions are conveyed to the brain.*

The *Nerves of the Spinal Cord* consist of thirty-one pairs, issuing from the sides of the whole length of the cord; their numbers corresponding with the intervertebral foramina through which they pass. Each nerve arises by two roots, an anterior and posterior, the latter being the largest. The roots emerge through separate apertures of the sheath of dura mater surrounding the cord; and directly after their emergence, while the roots lie in the intervertebral foramen, a ganglion is formed on the posterior root. The anterior root lies in contact with the anterior surface of the ganglion, but none of its fibres intermingle with those in the ganglion. But immediately beyond the ganglion, the two roots coalesce, and by the mingling of their fibres form a compound or mixed spinal nerve, which, after issuing from the intervertebral canal, divides into an anterior and posterior branch, each containing fibres from both the roots.

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* On the anatomy of the spinal cord consult any of the principal systematic treatises; or Grainger (ciii.); Todd (lxxiii. art. *Nervous centres*); Longet (cxxxvi.); Stilling and Wallach (clvii.); J. L. Clarke (xliii. 1851, 1853, and 1859); Kölliker (ccvi. ccxii. and ccxviii. 1860); Schrœder Van der Kolk (ccxix).

According to Kölliker (ccxviii. 1860, p. 244), the posterior root-fibres of the cord enter into no connection with the nerve-corpuscles in the ganglion, but pass directly through, in one or more bundles, which are collected into a trunk beyond the ganglion, and then join the motor root. From most, if not all, of the ganglionic corpuscles, one or two, rarely more, nerve-fibres arise and pass out of the ganglion, in a peripheral direction, in company with the posterior root-fibres of the cord. Each spinal ganglion, therefore, is to be regarded as a source of new nerve-fibres, which Kölliker names *ganglionic fibres*. The destination of these fibres is not yet determined: probably they pass especially into the vascular branches of the nerves which they accompany (Ib. p. 247).

The anterior root of each spinal nerve arises by numerous separate and converging fasciculi from the anterior column of the cord; the posterior root by more numerous parallel fasciculi, from the posterior column, or, rather from the posterior part of the lateral column; for if a fissure be directed inwards from the groove between the middle and posterior columns, the posterior roots will remain attached to the former. The anterior roots of each spinal nerve consist, exclusively of motor fibres; the posterior as exclusively of sensitive fibres. For the knowledge of this important fact, and much of the consequent progress of the physiology of the nervous system, science is indebted to Sir Charles Bell. The fact is proved in various ways. Division of the anterior roots of one or more nerves is followed by complete loss of motion in the parts supplied by the fibres of such roots; but the sensation of the same parts remains perfect. Division of the posterior roots destroys the sensibility of the parts supplied by their fibres, while the power of motion continues unimpaired. Moreover, irritation of the ends of the distal portions of the divided anterior roots of a nerve excites muscular movements; irritation of the ends of the proximal portions, which are still in connection with the cord, are followed by no effect. Irritation of the distal portions of the divided posterior roots, on the other hand, produces no

muscular movements, and no manifestation of pain; for, as already stated, sensitive nerves convey impressions only towards the nervous centres: but irritation of the proximal portions of these roots elicit signs of intense suffering. Occasionally, under this last irritation, muscular movements also ensue; but these are either voluntary, or the result of the irritation being reflected from the sensitive to the motor fibres. Occasionally, too, irritation of the distal ends of divided anterior roots elicits signs of pain, as well as producing muscular movements: the pain thus excited is probably the result of *cramp* (Brown-Séquard).

As an example of the experiments of which the preceding paragraph gives a summary account, this may be mentioned: If in a frog the three posterior roots of the nerves going to the hinder extremity be divided on the left side, and the three anterior roots of the corresponding nerves on the right side, the left extremity will be deprived of sensation, the right of motion. If the foot of the right leg, which is still endowed with sensation but not with the power of motion, be cut off, the frog will give evidence of feeling pain by movements of all parts of the body except the right leg itself, in which he feels the pain. If, on the contrary, the foot of the left leg which has the power of motion, but is deprived of sensation, is cut off, the frog does not feel it, and no movement follows, except the twitching of the muscles irritated by cutting them or their tendons.

### *Functions of the Spinal Cord.*

The spinal cord manifests all the properties already assigned to nervous centres (see p. 389).

1. It is capable of conducting impressions, or states of nervous excitement. Through it, the impressions made upon the peripheral extremities or other parts of the spinal sensitive nerves are conducted to the brain, where alone they

can be perceived by the mind. Through it, also, the stimulus of the will, applied to the brain, is capable of exciting the action of the muscles supplied from it with motor nerves. And for all these conductions of impressions to and fro between the brain and the spinal nerves, the perfect state of the cord is necessary; for when any part of it is destroyed, and its communication with the brain is interrupted, impressions on the sensitive nerves given off from it below the seat of injury, cease to be propagated to the brain; and the mind loses the power of voluntarily exciting the motor nerves proceeding from the portion of cord isolated from the brain.

Illustrations of this are furnished by various examples of paralysis, but by none better than by the common paraplegia, or loss of sensation and voluntary motion in the lower part of the body, in consequence of destructive disease or injury of a portion, including the whole thickness, of the spinal cord. Such lesions destroy the communication between the brain and all parts of the spinal cord below the seat of injury, and consequently cut off from their connection with the mind, the various organs supplied with nerves issuing from those parts of the cord. But if this lower portion of the cord preserves its integrity, the various parts of the body supplied with nerves from it, though cut off from the brain, will nevertheless be subject to the influence of the cord, and, as presently to be shown, will indicate its other powers as a nervous centre.

From what has been already said, it will appear probable that the conduction of impressions along the cord is effected (at least, for the most part) through the grey substance, *i.e.*, through the nerve-corpuscles and filaments connecting them. But there is reason to believe that all parts of the cord are not alike able to conduct all impressions; and that, rather, as there are separate nerve-fibres for motor and for sensitive impressions, so, in the cord, separate and determinate parts serve to conduct the same impressions. Until of late, it was

generally believed that the anterior and posterior columns of the cord, correspond to the anterior and posterior roots respectively; that the anterior contain only motor, the posterior only sensitive, fibres. The results of experiments by Longet and others, seemed to prove that division of the anterior and posterior columns, produced essentially the same effects as division of the anterior and posterior roots of the nerves. The important and philosophical labours of Dr. Brown-Séquard have, however, completely overturned this view, and cast new light on all relating to the functions of the spinal cord. It is not possible to do justice to these investigations in any summary, however lengthy and complete: the whole series, as delivered in lectures at the College of Surgeons, and published in the *Lancet*, of 1858, must be read and studied. An attempt will be made here, to point out only the principal conclusions deducible from them.

*a.* Sensitive impressions, conveyed to the spinal cord by root-fibres of the posterior nerves, are not conducted to the brain by the posterior columns of the cord, as hitherto has been generally supposed, but pass through them into the central grey substance; by which alone, or aided by the anterior columns, they are transmitted to the brain (fig. 48.)

*b.* The impressions thus conveyed to the grey substance, do not pass up to the brain along that half of the cord corresponding to the side from which they have been received; but, almost immediately after entering the cord, cross over to the other side, and along it are transmitted to the brain. There is thus, in the cord itself, a complete decussation of sensitive impressions brought to it; so that division or disease of one posterior half of the cord is followed by lost sensation, not in parts on the corresponding, but in those of the opposite side of the body.

*c.* The various sensations of touch, pain, temperature, and muscular contraction, are probably conducted along separate and distinct sets of fibres. All, however, undergo decussation

in the spinal cord, and along it are transmitted to the brain by the grey matter.

*d.* The posterior columns of the cord appear to have a great share in reflex movements, and this is the principal cause of the peculiar kind of paralysis so often observed in disease of these columns.

*e.* Impulses of the will, leading to voluntary contractions of muscles, appear to be transmitted principally along the anterior columns, and contiguous grey matter of the cord.

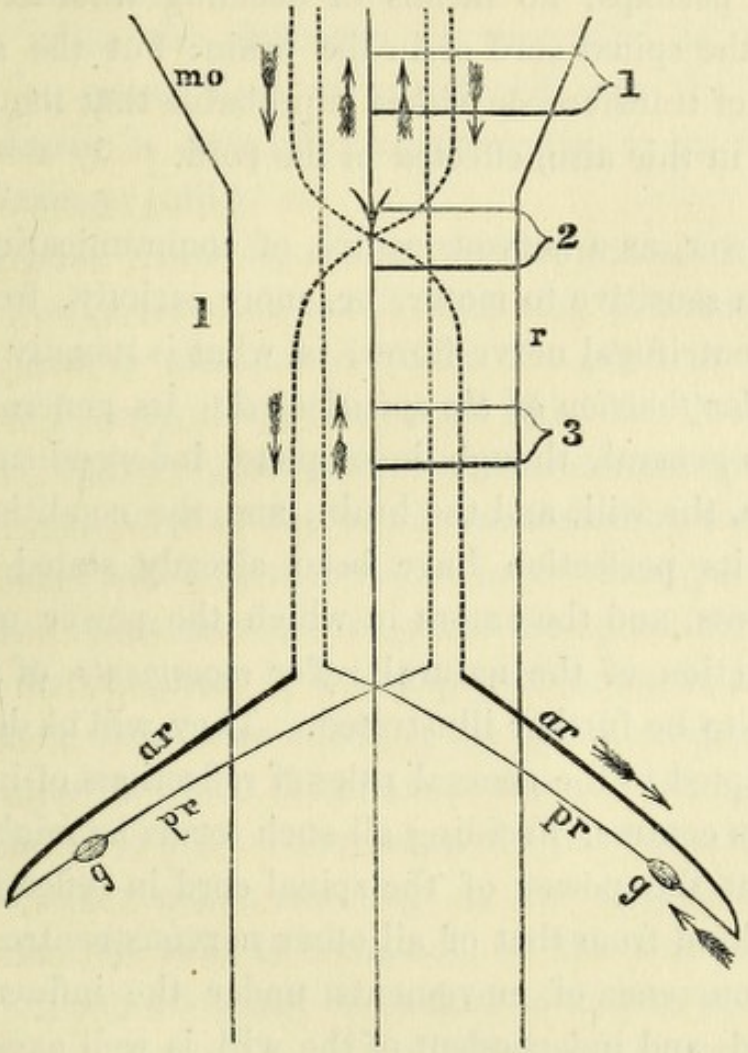
*f.* Decussation of motor impulses occurs, not in the spinal cord, as is the case with sensitive impressions, but, as hitherto admitted, at the anterior part of the medulla oblongata. This decussation, however, does not take place, as generally supposed, all along the median line, at the base of the encephalon, but only at the anterior pyramids, which are continuous with the lateral columns of the cord. Hence, the mandates of the will, having made their decussation, first enter the cord by the lateral tracts and adjoining grey matter, and then pass to the anterior columns and to the grey matter associated with them. Accordingly, division of the anterior pyramids, at the point of decussation, is followed by paralysis of motion in all parts below; while division of the olivary bodies, which constitute the true continuations of the anterior columns of the cord, appears to produce very little paralysis. Disease or division of any part of the cerebro-spinal axis *above* the seat of decussation is followed, as well-known, by impaired or lost power of motion on the *opposite* side of the body; while a like injury inflicted *below* this part, induces similar paralysis on the *corresponding* side.

2. In the second place, the spinal cord as a nervous centre, or rather, as an aggregate of many nervous centres, has the power of *communicating impressions* in the several ways already mentioned (p. 391).

Examples of the *transference* and *radiation* of impressions in the cord have been given; and that the transference at least

takes place in the cord, and not in the brain, is nearly proved by the case of pain felt in the knee, and not in the hip, in

*Fig.* 48.*




* The above diagram (after Brown-Séquard) explains the preceding statements, by representing the decussation of the conductors for voluntary movements, and those for sensations: *a r*, anterior roots and their continuations in the spinal cord, and decussation at the lower part of the medulla-oblongata, *m o*; *p r*, the posterior roots and their continuation and decussation in the spinal cord; *g g*, the ganglions of these roots. The arrows indicate the direction of the nervous action: *r*, the right side; *l*, the left side. 1, 2, 3, indicate places of alteration in a lateral half of the spino-cerebral axis, to shew the influence on the two kinds of conductors, resulting from section of the cord at either of these three places.

diseases of the hip; of pain felt in the urethra or glans penis, and not in the bladder, in calculus; for, if both the primary, and the secondary or transferred impressions, were in the brain, both should be always felt. Of radiation of impressions, there are, perhaps, no means of deciding whether they take place in the spinal cord or in the brain: but the analogy of the cases of transference makes it probable that the communication is, in this also, effected in the cord.

The power, as a nervous centre, of communicating impressions from sensitive to motor, or, more strictly, from centripetal to centrifugal nerve-fibres, is what is usually discussed as the *reflex function of the spinal cord.* Its general mode of action, its general, though incomplete, independence of consciousness, the will, and the brain, and the conditions necessary for its perfection have been already stated (p. 394). These points, and the extent in which the power operates in the production of the natural *reflex movements* of the body, have now to be further illustrated. They will be described in terms adapted to the general rules of reflections of impressions in nervous centres, avoiding all such terms as might seem to imply that the power of the spinal cord in reflecting, is different in kind from that of all other nervous centres.

The occurrence of movements under the influence of the spinal cord, and independent of the will, is well exemplified in the acts of swallowing, in which a portion of food carried by voluntary efforts into the fauces, is conveyed by successive involuntary contractions of the constrictors of the pharynx and muscular walls of the œsophagus into the stomach. These contractions are excited by the stimulus of the food on the centripetal nerves of the pharynx and œsophagus being first conducted to the spinal cord and medulla oblongata, and thence reflected through the motor nerves of these parts.*

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* It is customary to call the nerves thus conducting impressions to be reflected, *excito-motory;* and the nerves by which the impressions are

All these movements of the pharynx and œsophagus are involuntary; the will cannot arrest them or modify them; and though the mind has a certain consciousness of the food passing, which becomes less as the food passes further; yet that this is not necessary to the act of deglutition, is shown by its occurring when the influence of the mind is completely removed; as when food is introduced into the fauces or pharynx during a state of complete coma, or in a brainless animal (Grainger, clii.).

So, also, for example, under the influence of the spinal cord, the involuntary and unfelt muscular contraction of the sphincter ani is maintained when the mind is completely inactive, as in deep sleep, but ceases when the lower part of the cord is destroyed, and cannot be maintained by the will.

The independence of the mind manifested by the reflecting power of the cord, is further shown in the most perfect occurrence of the reflex movements, when the spinal cord and the brain are disconnected, as in decapitated animals, and in cases of injuries or diseases so affecting the spinal cord, as to divide or disorganise its whole thickness at any part whose perfection is not essential to life. Thus, when the head of a lizard is cut off, the trunk remains standing on the feet, and the body writhes when the skin is irritated. If the animal is cut in two, the lower portion can be excited to motion as well as the upper portion; the tail may be divided into several segments, and each segment, in which any portion of spinal cord is contained, contracts on the slightest touch; even the extremity of the tail moves as before, as soon as it is touched. All the

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reflected, *reflecto-motory;* and corresponding terms are applied in explanation of the reflex acts of the cord. They are here avoided, both for the reason given in the preceding paragraph, and because they are apt to lead the student to believe that the nerves contain one set of fibres for the conduction of impressions to and from the brain, and another for the conduction of them to and from the spinal cord; the improbability of which will appear from what is said of the structure of the cord in p. 397.

portion of the animal in which these movements can be excited, contain some part of the spinal cord; and it is evidently the cause of the motions excited by touching the surface; for they cannot be excited in parts of the animal, however large, if no part of the cord is contained in them. Mechanical irritation of the skin excites not the slightest motion in the leg when it is separated from the body; yet the extremity of the tail moves as soon as it is touched. With the same power of the spinal cord in reflecting impressions, an eel, or a frog, or any other cold-blooded animal, will move along after it is deprived of its head, and when, however much the movements may indicate purpose, it is not probable that consciousness or will has any share in them. And so, in the human subject, or any warm-blooded animal, when the cord is completely divided across, or so diseased at some part that the influence of the mind cannot be conveyed to the parts below it, the irritation of any part of the surface supplied by nerves given off from the cord below the seat of injury, is commonly followed by spasmodic and irregular reflex movements, even though in the healthy state of the cord, such involuntary movements could not be excited when the attention of the mind was directed to the irritating cause.

In the fact last-mentioned, is an illustration of an important difference between the warm-blooded and the lower animals in regard to the reflecting power of the spinal cord (or its homologue in the Invertebrata), and the share which it and the brain have respectively, in determining the several natural movements of the body. When, for example, a frog's head is cut off, the limbs remain in or assume a natural position; resume it when disturbed; and when the abdomen or back is irritated, the feet are moved with the manifest purpose of pushing away the irritation. It is as if the mind of the animal were still engaged in the acts.* But, in division of the

* The evident adaptation and purpose in the movements of the cold-blooded animals, have led some to think that they must be conscious and

human spinal cord, the lower extremities fall into any position that their weight and the resistance of surrounding objects combine to give them; if the body is irritated, they do not move towards the irritation; and if themselves are touched, the consequent movements are disorderly and purposeless. Now, if we are justified by analogy in assuming that the will of the frog cannot act more than the will of man, through the spinal cord separated from the brain, then it must be admitted, that many more of the natural and purposive movements of the body can be performed under the sole influence of the cord in the frog than in man; and what is true in the instances of these two species, is generally true also of the whole class of cold-blooded as distinguished from warm-blooded animals. It may not, indeed, be assumed that the acts of standing, leaping, and other movements, which decapitated cold-blooded animals can perform, are also always, in the entire and healthy state, performed involuntarily, and under the sole influence of the cord; but it is probable that such acts may be, and commonly are, so performed, the mind of the animal having only the same kind of influence in modifying and directing them, as the mind of man has in modifying and directing the movements of the respiratory muscles.

The fact that such movements as are produced by irritating the skin of the lower extremities in the human subject, after division or disorganization of a part of the spinal cord, do not follow the same irritation when the mind is active and connected with the cord through the brain, is, probably, due to the mind ordinarily perceiving the irritation and instantly controlling the muscles of the irritated and other parts; for, even when the cord is perfect, such involuntary movements will often follow irritation if it be applied when the mind is wholly

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capable of will without their brains. But purposive movements are no proof of consciousness or will in the creature manifesting them. The movements of the limbs of headless frogs are not more purposive than the movements of our own respiratory muscles are: in which we know that neither will nor consciousness is at all times concerned.

occupied. When, for example, one is anxiously thinking, even slight stimuli will produce involuntary and reflex movements. So, also, during sleep, such reflex movements may be observed when the skin is touched or tickled; for example, when one touches with a finger the palm of the hand of a sleeping child, the finger is grasped—the impression on the skin of the palm producing a reflex movement of the muscles which close the hand. But when the child is awake, no such effect is produced by a similar touch.

On the whole, it may, from these and like facts, be concluded, that the proper reflex acts, performed under the influence of the reflecting power of the spinal cord, are essentially independent of the brain, and may be performed perfectly when the brain is separated from the cord: that these include a much larger number of the natural and purposive movements of the lower animals than of the warm-blooded animals and man: and that over nearly all of them the mind may exercise, through the brain, some control; determining, directing, hindering, or modifying them, either by direct action or by its power over associated muscles.

In this fact, that the reflex movements from the cord may be perfectly performed without the intervention of consciousness or will, yet are amenable to the control of the will, we may see their admirable adaptation to the well-being of the body. Thus, for example, the respiratory movements may be performed while the mind is, in other things, fully occupied, or in sleep powerless; yet, in an emergency, the mind can direct and strengthen them: and it can adapt them to the several acts of speech, effort, etc. Being, for ordinary purposes, independent of the will and consciousness, they are performed perfectly, without experience or education of the mind; yet they may be employed to other and extraordinary uses when the mind wills, and so far as it acquires power over them. Being commonly independent of the brain, their constant continuance does not produce weariness; for it is only in the brain that it or any other sensation can be perceived.

The subjection of the muscles to both the spinal cord and the brain, makes it difficult to determine in man what movements or what share in any of them can be assigned to the reflecting power of the cord. The fact, that after division or disorganisation of a part of the cord, movements, and even forcible though purposeless ones, are produced in the lower limbs when the skin is irritated, proves that the spinal cord can supply nervous force for the action of the muscles that are, naturally, most under the control of the will: and it is, therefore, not improbable, that, for even the voluntary action of those muscles, when the cord is perfect, it may supply the force, and the will the direction. As instances in which it supplies both force and direction, that is, both excites and determines the combination of muscles, may be mentioned the acts of the abdominal muscles in vomiting and voiding the contents of the bladder and rectum: in both of which, though, after the period of infancy, the mind may have the power of postponing or modifying the act, there are all the evidences of reflex action; namely, the necessary precedence of a stimulus, the independence of the will, and, sometimes, of consciousness, the combination of many muscles, the perfection of the act without the help of education or experience, and its failure or imperfection in disease of the lower part of the cord. The emission of semen is equally a reflex act governed by the spinal cord: the irritation of the glans penis conducted to the spinal cord, and thence reflected, excites the successive and co-ordinate contractions of the muscular fibres of the vasa deferentia and vesiculæ seminales, and of the bulbo-cavernosi and other muscles of the urethra; and a forcible expulsion of semen takes place, over which the mind has little or no control, and which, in cases of paraplegia, may be unfelt. The erection of the penis also, as already explained (page 144), appears to be in part the result of a reflex contraction of the muscles by which the veins returning the blood from the penis are compressed. Irritation of the vagina in sexual intercourse appears also to be propagated to the spinal cord, and

thence reflected to the motor nerves supplying the Fallopian tubes. The involuntary action of the uterus in expelling its contents during parturition, is also of a purely reflex kind, dependent in part upon the spinal cord, though in part also upon the sympathetic system: its independence of the brain and the mind was proved by cases of delivery in paraplegic women, and is now more abundantly shewn in the use of chloroform.

Besides these acts regularly performed under the influence of the reflecting power of the spinal cord, others are manifested in accidents; such as the movement of the limbs and other parts, to guard the body against the effects of sudden danger. When, for example, a limb is pricked or struck, it is instantly and involuntarily withdrawn from the instrument of injury; a threatened blow on the face causes involuntary closure of the eye. And the same preservative tendency of the reflex power of the cord is shewn in the outstretched arms when falling forwards, and their reversed position when falling backwards.

To these instances of spinal reflex action, some add yet many more, including nearly all the acts which seem to be performed unconsciously, such as those of standing, walking, and the like. But these are not involuntary acts; they are not accomplished without the active co-operation of the brain, for they are impossible in coma, sleep, paraplegia, and complete mental abstraction; they all require education for their perfection; their force is not proportioned to any external stimulus exciting them; they produce weariness; in short, they appear to be only examples how small an amount of attention and will are necessary for the performance of habitual acts.

The phenomena of spinal reflex actions in man are much more striking and unmixed in cases of disease. In some of these, the effect of a morbid irritation, or a morbid irritability of the cord, is very simple; as when the local irritation of

sensitive fibres, being propagated to the spinal cord, excites merely local spasms,—spasms, namely, of those muscles, the motor fibres of which arise from the same part of the spinal cord as the sensitive fibres that are irritated. Of such a case we have instances in the spasms and tremors of limbs on which a severe burn is inflicted, etc.

In other instances, in which we must assume that the cord is morbidly more irritable, *i.e.*, apt to issue more nervous force than is proportionate to the stimulus applied to it, a slight impression on a sensitive nerve produces extensive reflex movements. This appears to be the condition in tetanus, in which a slight touch on the skin may throw the whole body into convulsion. A similar state is induced by the introduction of strychnia, and, in frogs, of opium, into the blood; and numerous experiments on frogs thus made tetanic have shown that the tetanus is wholly unconnected with the brain, and depends on the state induced in the spinal cord.

It may have seemed to be implied that the spinal cord as a single nervous centre, reflects alike from all parts all the impressions conducted to it. But it is more probable that it should be regarded as a collection of nervous centres united in a continuous column. This is made probable by the fact that segments of the cord may act as distinct nervous centres, and excite motions in the parts supplied with nerves given off from them; as well as by the analogy of certain cases in which the muscular movements of single organs are under the control of certain circumscribed portions of the cord. Thus Volkmann (lxxx. 1844) has shewn that the rhythmical movements of the anterior pair of lymphatic hearts in the frog depend upon nervous influence derived from the portion of spinal cord corresponding to the third vertebra, and those of the posterior pair on influence supplied by the portion of cord opposite the eighth vertebra. The movements of the heart continue, though the whole of the cord, except the above portions, be destroyed; but on the instant of destroying either of these

portions, though all the rest of the cord is untouched, the movements of the corresponding hearts cease. What appears to be thus proved in regard to two portions of the cord, may be inferred to prevail in other portions also; and the inference is reconcilable with most of the facts known concerning the physiology and comparative anatomy of the cord.

The influence of the spinal cord on the sphincter ani has been already mentioned (p. 407). It maintains this muscle in permanent contraction, so that, except in the act of defecation, the orifice of the anus is always closed. This influence of the cord resembles its common reflex action in being involuntary, although the will can act on the muscle to make it contract more or to permit its dilatation, and in that the constant action of the muscle is not felt, nor diminished in sleep, nor productive of fatigue. But the act is different from ordinary reflex acts in being nearly constant. In this respect, it resembles that condition of muscles which has been called *Tone*,* or passive contraction; in a state in which they always appear to be when not active in health, and in which, though called inactive, they appear to be in slight contraction, and certainly are not relaxed, as they are long after death, or when the spinal cord is destroyed. This tone of all the muscles of the trunk and limbs seems to depend on the spinal cord, as the contraction of the sphincter ani does. If an animal is killed by injury or removal of the brain, the tone of the muscles may be left, and the limbs feel firm as during sleep; but if the spinal cord be destroyed, the sphincter ani relaxes, and all the muscles feel loose, and flabby, and atonic, and remain so till the rigor mortis commences.

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* This kind of tone must be distinguished from that mere firmness and tension which it is customary to ascribe with the name of *tone* to all tissues that feel robust and not flabby, as well as to muscles. The tone peculiar to muscles has in it a degree of vital contraction: that of other tissues is only due to their being well nourished, and therefore compact and tense.

For the further study of the functions of the spinal cord, it need scarcely be said, that the works of Sir Charles Bell and Dr. Marshall Hall are the most important. The other principal writings are those of Prochaska (cliii.); Magendie (clv.); Müller (xxxii.); Grainger (clii.); Newport (xliii. 1844); Volkmann (lxxx. 1838); Dr. W. Budd (xli. vol. xxii.); Carpenter (cxxxi.); Todd (lxxiii. art. *Nervous Centres*); Barlow (lxxi. vol. xli.); Brown-Séquard (cxc. April, 1856, and xxx. 1858); and Schrœder Van de Kolk (ccxix.).

## THE MEDULLA OBLONGATA.

### *Its Structure.*

The medulla oblongata is a mass of grey and white nervous substance partly contained within the cavity of the cranium, forming a portion of the cephalic prolongation of the spinal cord, and connecting it with the brain. The grey substance which it contains is situated in the interior, variously divided into masses and laminæ by the white or fibrous substance which is arranged partly in external columns, and partly in fasciculi traversing the central grey matter. The medulla oblongata is larger than any part of the spinal cord. Its columns are pyriform, enlarging as they proceed towards the brain, continuous with those of the spinal cord, more prominent than they are, and separated from one another by deeper grooves. In front are two, corresponding with the anterior columns of the cords, and named *anterior pyramids*, or *corpora pyramidalia*; they are separated from each other by a deep, anterior, median fissure, at the bottom of which fibres appear decussating, i. e., crossing one another and changing sides. In this manner, nearly all the fibres of each pyramid pass over, and, turning backwards become continuous with the opposite lateral columns of the cord; those which do not decussate are directly continuous with the anterior column of the cord. Traced upwards, the fibres of the anterior pyramids pass through the inferior part

of the pons Varolii; and then forming the lower part of the crura cerebri, proceed through the optic thalami and corpora striata, to be distributed in the substance of the cerebral hemispheres.*

External to each anterior pyramid is a prominent oval body (the *olivary body*), the fibres in and around which are continuous below with those of the corresponding anterior tracts of the cord, while above they pass into the deeper longitudinal fibres of the medulla oblongata, along which they may be traced through the crura cerebri into the lower parts of the optic thalami and corpora striata. The *corpora olivaria* are formed of portions of grey substance imbedded in fibres, and elevating them.

Immediately behind the corpora olivaria, on each side is a small, depressed tract, of fibrous matter, distinguished from the olivary tract because its fibres, instead of passing onwards longitudinally to the cerebrum, go outwards transversely through the pons into the cerebellum. These tracts are named the *lateral tracts*, and are interesting in that the facial nerve emerges through them, and probably derives from them its connection with the motor portion of the medulla oblongata and cord.

Behind the lateral tract on each side is the *corpus restiforme*, a large column of nerve-fibres, which, with its continued fibres below, forms the *restiform tract*. It is continuous below

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* The expressions "continuous fibres," and the like, appear to be usually understood as meaning that certain primitive nerve-fibres pass without interruption from one part to another. But such continuity of primitive fibres through long distances in the nervous centres is very far from proved. The apparent continuity of fasciculi (which is all that dissection can yet trace) is explicable on the supposition that many comparatively short fibres lie parallel, with the ends of each inlaid among many others. In such a case, there would be an apparent continuity of fibres; just as there is, for example, when one untwists and picks out a long cord of silk or wool, in which each fibre is short, and yet each fasciculus appears to be continued through the whole cord.

with the posterior columns of the cord, while above, its fibres may be traced transversely through the pons into the cerebellum. Those of each body form a large portion of the corresponding crus cerebelli, and are distributed to the corresponding hemisphere of the cerebellum, whence it is probable that continuations from them pass into the cerebrum.

The restiform bodies are separated from each other posteriorly by two narrow columns, the *posterior pyramids*, or *posterior pyramidal tracts*, one on each side of the posterior fissure; and by the lower angle of the fourth ventricle. The fibres of these tracts are continuous below with a narrow column, which about the middle of the cervical portion of the cord begins to be, as it were, set off from the posterior columns by a narrow groove. They seem to pass upwards, longitudinally, through the pons, and thence in connection with the processes that unite the cerebrum with the cerebellum, under the corpora quadrigemina, and into the crus cerebri of the opposite side.

Deeper than the posterior pyramidal tracts, and forming slight elevations on each side of the middle line of the fourth ventricle, are other two, named the *round tracts*. They appear to be composed of the middle or axial portions of the anterior and lateral columns, which, as they pass upwards, are, as it were, exposed from behind by the divergence of the restiform and posterior pyramidal tracts. The round tracts pass longitudinally through the pons, and thence proceed, decussating, under the corpora quadrigemina to the fibres of the crura cerebri.

The continuation of the grey matter of the cord into the medulla oblongata forms the grey matter covering the floor of the fourth ventricle, and diffused beneath its surface. The separation of the posterior internal and restiform tracts leaves open, in the fourth ventricle, the upper portion of the canal which, in the early fœtal state, extends through the whole length of the grey matter of the spinal cord, and is continuous above with the cerebral ventricles.

It is unfortunate that even a much deeper study than is here sketched of the anatomy of the medulla oblongata, affords very little insight into its physiology. The interest connected with the tracing of the continuities of its several columns with those of the spinal cord lies, chiefly, in the fact that nerves of similar function arise from both. Thus, from the anterior pyramids, and their continuation in the crura cerebri, arise the motor third and sixth pairs of cerebral nerves. From the groove between the anterior pyramids and the olivary tracts (a groove continuous with that in which all the motor roots of the spinal nerves emerge), arises the motor hypoglossal nerve. From the lateral and the round tracts, formed of fibres continuous with the anterior and lateral columns of the cord, arise the motor facial, and fourth or trochlear nerves; while from the front of the restiform tracts, in a line continuous with the groove between the posterior and lateral columns of the cord, spring the roots of the sensitive glosso-pharyngeal and pneumogastric nerves.

There is, thus, the closest analogy in structure and, probably also, in the general endowments of their several parts, between the medulla oblongata and the spinal cord. The difference in size and form appears due, chiefly, first, to the divergence, enlargement, and decussation of the several columns, as they pass to be connected with the cerebellum or the cerebrum; and, secondly, to the insertion of new quantities of grey matter, in the olivary bodies and other parts, in adaptation to the higher office, and wider range of influence, which the medulla oblongata as a nervous centre exercises.*

### *Functions of the Medulla Oblongata.*

In its functions, the medulla oblongata differs from the spinal cord chiefly in the importance and extent of the actions that it

* For the latest accounts of the structure of the medulla oblongata see Lockhart Clarke (xliii. 1858), and Schroeder Van der Kolk (ccxix.).

governs. Like the cord, it may be regarded first, as *conducting* impressions, in which office it has a wider extent of function than any other part of the nervous system, since it is obvious that all impressions passing to and fro between the brain and the spinal cord and all nerves arising below the pons, must be transmitted through it. The decussation of part of the fibres of the anterior pyramids of the medulla oblongata explains the phenomena of cross-paralysis, as it is termed, *i.e.*, of the loss of motion, in cerebral apoplexy, being always on the side opposite to that on which the effusion of blood has taken place. Looking only to the anatomy of the medulla oblongata, it was not possible to explain why the loss of sensation also is on the side opposite the injury or disease of the brain: for there is no evidence of a decussation of posterior fibres like that which ensues among the anterior fibres of the medulla oblongata. But the discoveries of Brown-Séquard have shewn that the crossing of sensitive impressions occurs in the spinal cord (see p. 405).

The functions of the medulla oblongata as a *nervous centre*, seem to be more immediately important to the maintenance of life than those of any other part of the nervous system, since from it alone, or in chief measure, appears to issue the nervous force necessary for the performance of respiration and deglutition. It has been proved by repeated experiments, especially by those of Legallois (cxxxix. t. i. 64), Flourens (cxl.), and Longet (cxxxvi.), that the entire brain may be gradually cut away in successive portions, and yet life may continue for a considerable time, and the respiratory movements be uninterrupted. Life may, also, continue when the spinal cord is cut away in successive portions from below upwards as high as the point of origin of the phrenic nerve, or in animals without a diaphragm, such as birds or reptiles, even as high as the medulla oblongata. In Amphibia, these two experiments have been combined: the brain being all removed from above, and the cord from below; and so long as the medulla oblongata was intact, respiration and life were maintained.

But if, in any animal, the medulla oblongata is wounded, particularly if it is wounded in its central part, opposite the origin of the pneumogastric nerves, the respiratory movements cease, and the animal dies as if asphyxiated. And this effect ensues even when all parts of the nervous system, except the medulla oblongata, are left intact.

Injury and disease in men prove the same as these experiments on animals. Numerous instances are recorded, especially by Sir Charles Bell (cxlii.), in which injury to the human medulla oblongata has produced instantaneous death; and, indeed, it is through injury of it, or of the part of the cord connecting it with the origin of the phrenic nerve, that death is commonly produced in fractures and diseases with sudden displacement of the upper cervical vertebræ.

The centre whence the nervous force for the production of combined respiratory movements appears to issue is in the interior of that part of the medulla oblongata from which the pneumogastric nerves arise; for with care the medulla oblongata may be divided to within a few lines of this part, and its exterior may be removed, without the stoppage of respiration; but it immediately ceases when this part is invaded. This is not because the integrity of the pneumogastric nerves is essential to the respiratory movements; for both these nerves may be divided without more immediate effect than a retardation of these movements. The conclusion, therefore, may safely be, that this part of the medulla oblongata is the nervous centre wherein the impulses producing the respiratory movements chiefly originate, and whence they issue in rhythm and adaptation.*

* Dr. Brown Séquard has of late (ccxiv. 1858, p. 600) brought forward some important evidence, to shew that the impulses leading to the respiratory movements do not originate exclusively in the medulla oblongata, but that they issue also from all the other *incito-motory* parts of the cerebro-spinal axis and from the grey matter which connects those parts with the motor nerves going to the respiratory muscles. The influence of the medulla oblongata upon the respiratory movements is, however, undoubtedly so great, that there probably need be no hesitation in adopting the general conclusion stated above.

The power by which the medulla oblongata governs and combines the action of various muscles for the respiratory movements is an instance of the power of *reflection*, which it possesses in common with all nervous centres. Its general mode of action, as well as the degree in which the mind may take part in respiration, and the number of nerves and muscles which, under the governance of the medulla oblongata, may be combined in the forcible respiratory movements, have been already briefly described (see pp. 174-5). That which seems most peculiar in this centre of respiratory action is its wide range of connection, the number of nerves by which the centripetal impression to excite motion may be conducted, and the number and distance of those through which the motor impulse may be directed. The principal centripetal nerves engaged in respiration are the pneumogastric, whose branches supplying the lungs appear to convey the most acute impression of the "necessity of breathing." When they are both divided the respiration becomes slower (J. Reid, xciv. 1838), as if the necessity were less acutely felt: but it does not cease, and therefore other nerves besides them must have the power of conducting the like impression. The experiments of Volkmann make it probable that all centripetal nerves possess it in some degree, and that the existence of imperfectly aerated blood in contact with any of them acts as a stimulus, which, being conveyed to the medulla oblongata, is reflected to the nerves of the respiratory muscles: so that respiratory movements do not wholly cease so long as any centripetal nerves, and any nerves supplying muscles of respiration, are both in continuous connection with the respiratory centre of the medulla oblongata.

The wide extent of connection which belongs to the medulla oblongata as the centre of the respiratory movements, is further shewn by the fact, that impressions, by mechanical and other ordinary stimuli, made on many parts of the external or internal surface of the body, may induce respiratory movements. Thus involuntary inspirations are induced by the sudden con-

tact of cold with any part of the skin, as in dashing cold water into the face. Irritation of the mucous membrane of the nose produces sneezing. Irritation in the pharynx, œsophagus, stomach, or intestines, excites the concurrence of the respiratory movements to produce vomiting. Violent irritation in the rectum, bladder, or uterus, gives rise to a concurrent action of the respiratory muscles, so as to effect the expulsion of the fæces, urine, or fœtus.

The medulla oblongata appears to be the centre whence are derived the motor impulses enabling the muscles of the palate, pharynx, and œsophagus, to produce the successive co-ordinate and adapted movements necessary to the act of *deglutition* (see pp. 204-5). This is proved by the persistence of the power of swallowing after destruction of the cerebral hemispheres and cerebellum; its existence in anencephalous monsters; the power of swallowing possessed by marsupial embryoes before the brain is developed; and by the complete arrest of the power of swallowing when the medulla oblongata is injured in experiments. But the reflecting power herein exercised by the medulla oblongata is of a much simpler and more restricted kind than that exercised in respiration; it is, indeed, not more than a simple instance of reflex action by a segment of the spinal axis, receiving impressions for this purpose from only a few centripetal nerves, and reflecting them to the motor nerves of the same organ. The incident or centripetal nerves in this case are the branches of the glosso-pharyngeal and, in a subordinate degree, those of the cervical nerves, which combine to form the pharyngeal plexus; and the nerves through which the motor impressions to the fauces and pharynx are reflected are the pharyngeal branches of the vagus, and, in subordinate degrees, or as supplying muscles accessory to the movements of the pharynx, the branches of the hypoglossal, facial, cervical, recurrent and fifth nerves. For the œsophageal movements, so far as they are connected with the medulla oblongata, the filaments of the pneumogastric nerve alone appear to be sufficient (see John Reid, xciv. 1838).

Though respiration and life continue while the medulla oblongata is perfect and in connexion with respiratory nerves, yet, when all the brain above it is removed, there is no more appearance of sensation, or will, or of any mental act in the animal the subject of the experiment, than there is when only the spinal cord is left. The movements are all involuntary and unfelt; and the medulla oblongata has therefore no claim to be considered as an organ of the mind, or as the seat of sensation or voluntary power. These are connected with parts next to be described.

It may be here observed, that the part of the medulla oblongata which acts as a nervous centre, may continue to discharge its function after the part which is only a conductor has ceased to act. Thus, patients with apoplexy or compression of the brain may go on breathing, though, if they have any sensibility or voluntary power, it is so little, that we cannot suppose any impressions to be conveyed, in either direction, through the medulla oblongata. And so, when ether or chloroform has been inhaled, patients breathe very well, though they are so wholly insensible, and have so completely lost all voluntary power, that we cannot suppose the medulla oblongata to conduct either to or from the pons or any other part of the brain.

Moreover, it appears, that by such inhalation much of the reflecting power of the medulla oblongata may be destroyed; and yet its power in the respiratory movements may remain. Thus, in patients completely affected with chloroform, the winking of the eye-lids ceases, and irritation of the pharynx will not produce the usual movements of swallowing, or the closure of the glottis (so that blood may run quietly into the stomach, or even into the lungs); yet, with all this, they may breathe steadily, and shew that the power of the medulla oblongata to combine in action all the nerves of the respiratory muscles is perfect (see Longet, cxxii. 1847).

In addition to its influence over the functions of respiration and deglutition, the medulla oblongata appears to be largely

concerned, also, in the faculty of speech. Schroeder Van der Kolk has of late especially developed this view, and brought forward much evidence to prove that the corpora olivaria are accessory ganglia, the main use of which is to communicate simultaneously to the hypoglossal nerves, the multitudinous combinations of muscular movements required in speech, and thus to produce a uniform action of both sides of the tongue (ccxix.)

## STRUCTURE AND PHYSIOLOGY OF THE MESO-CEPHALON, OR PONS VAROLII.

The encephalon, or brain, is usually divided in anatomical description, into four parts, namely, the medulla oblongata, the meso-cephalon (pons, pons Varolii, or tuber annulare), the cerebellum, and the cerebrum. The meso-cephalon, or pons, is composed principally of transverse fibres connecting the two hemispheres of the cerebellum, and forming its principal commissure. But it includes, interlacing with these, numerous longitudinal fibres which connect the medulla oblongata with the cerebrum, and transverse fibres which connect it with the cerebellum. Among the longitudinal fibres of the pons, the inferior and some of the superior connect the anterior pyramidal, the olivary, and the round tracts of the medulla oblongata with the cerebrum; while others of the superior fibres connect with it the posterior and internal columns of the medulla. By the transverse fibres of the pons, a part of the anterior and lateral tracts, and, apparently, the whole of the restiform tracts of the medulla oblongata, are connected with the cerebellum; so that the pons may be regarded as containing the several means, 1st, by which the cerebrum is connected with all the tracts of the medulla oblongata, except the restiform and lateral; 2nd, by which the cerebellum is connected with these two tracts; 3rd, those by which its two hemispheres are united; and, lastly, (if we may reckon the *processus arciformes*

or *ponticulus* as part of the pons), the fibres by which the anterior pyramidal and the restiform tracts of the medulla oblongata are connected with each other. And among the fasciculi of nerve-fibres by which these several parts are connected, the pons also contains abundant grey or vesicular substance, which appears irregularly placed among the fibres, and fills up all the interstices.

As a conductor of impressions, we may consider the pons, as its anatomy would suggest, to contain the continuation of the conducting portion of the medulla oblongata to the cerebrum and cerebellum.

As a nervous centre, it appears probable that the pons may be regarded as the first, or lowest portion of the encephalon, in which, when the rest of the brain is removed, the mind may have sensation of impressions or exercise the will. When all the encephalon above the medulla oblongata is removed from a warm-blooded animal, it appears absolutely insensible, and deprived of all voluntary power; it only breathes and has other, generally purposeless, reflex movements of the trunk and limbs. But experiments of Flourens and Longet shew that when the pons is left, with the medulla oblongata, indications of sensibility may be elicited, and the movements that follow them are characteristic of purpose and will. Thus, in the experiments on rabbits and puppies, the cerebrum and cerebellum being removed, with the corpora striata, and all other parts down to the pons, when the tail was pinched the creature cried out, when ammonia was held to its nose it put up its foot to remove the irritation. So long as it was not irritated it remained passive and motionless; but it resisted irritation, and when disturbed from an apparently easy posture, resumed it. All these movements ceased as soon as the pons was removed. It must, therefore, be assumed either that the pons is an organ through which the mind may receive and transmit impressions, or that it is a nervous centre for higher and more purposive reflex acts, than the medulla oblongata or any part

of the spinal cord. The latter may be the true explanation of the movements above-described, for they are not more indicative of sensation and will than are those of the decapitated frog, in which there is sufficient reason to believe that neither of these mental faculties subsists; but, to believe that these movements are voluntary and expressive of sensations, appears more accordant with the general fact of the subordination of the reflex function to the power of the will in the warm-blooded animals.

### STRUCTURE AND PHYSIOLOGY OF THE CEREBELLUM.

The more one ascends towards the highest organs of the cerebro-spinal system, the more difficult does it become to trace any structure beyond that of external form and connection, and much more difficult to connect even the manifest structure with any of the functions of the part. With reference to the cerebellum, there appears, at present, so complete a want of connection between its anatomy and its physiology, that it would not assist in the design of this work to say more of the former, than that each of the lateral lobes or hemispheres of which it mainly consists, appears formed on the prolongations of fibres combined in a *crus cerebelli;* that these fibres are derived from three sources, namely, 1st. The restiform tracts of the medulla oblongata forming the *inferior* crus or peduncle; 2nd. Interchanging or commissural fibres, which, together with fibres going outwards from the lateral tracts of the medulla oblongata, form the *middle* crus, or peduncle; 3rdly. Fibres interchanging between the cerebellum and cerebrum, which form the *superior* crus, or *processus a cerebello ad testem.* Further, that the prolongation of the crus cerebelli, in which these three fasciculi are combined, contains, imbedded in it, a mass of grey matter, the *corpus dentatum,* and sends off lamellæ, which separate and are arranged like the nervules of a leaf, and are overlaid with layers of grey matter, folded and closely

adjusted over the ends of the nervules. The pons, as already said, forms the inferior and principal commissure connecting the two hemispheres of the cerebellum; but they are also united above, by a continuity of both grey and white substance, arranged on the same general plan as in themselves, in the *vermiform processes.*

The physiology of the cerebellum may be considered in its relation to sensation, voluntary motion, and the instincts or higher faculties of the mind. It is itself insensible to irritation, and may be all cut away without eliciting signs of pain (Longet, cxxxvi. t. i. 733, and others). Yet, if any of its crura be touched, pain is indicated; and, if the restiform tracts of the medulla oblongata be irritated, the most acute suffering appears to be produced. Its removal or disorganisation by disease is, also, generally unaccompanied with loss or disorder of sensibility; animals from which it is removed can smell, see, hear, and feel pain, to all appearance, as perfectly as before (Flourens, cxl.; Magendie, cxli, etc.). So that, although the restiform tracts of the medulla oblongata, which themselves appear so sensitive, enter the cerebellum, it cannot be regarded as a principal organ of sensibility.

In reference to motion, the experiments of Longet and most others agree, that no irritation of the cerebellum produces movement of any kind. Remarkable results however, are produced by removing parts of its substance. Flourens (whose experiments have been abundantly confirmed by those of Bouillaud (clxxvi), Longet (cxxxvi. t. i. 740), and others) extirpated the cerebellum in birds by successive layers. Feebleness and want of harmony of the movements were the consequence of removing the superficial layers. When he reached the middle layers, the animals became restless without being convulsed; their movements were violent and irregular, but their sight and hearing were perfect. By the time that the last portion of the organ was cut away, the animals had entirely lost the powers of springing, flying, walking, standing, and preserving their equilibrium. When an animal in this

state was laid upon its back, it could not recover its former posture; but it fluttered its wings, and did not lie in a state of stupor; it saw the blow that threatened it, and endeavoured to avoid it. Volition, sensation, and memory, therefore, were not lost, but merely the faculty of combining the actions of the muscles; and the endeavours of the animal to maintain its balance were like those of a drunken man.

The experiments afforded the same results when repeated on all classes of animals, and, from them and the others before referred to, Flourens inferred that the cerebellum belongs neither to the sensitive nor the intellectual apparatus; and that it is not the source of voluntary movements, although it belongs to the motor-apparatus: but is the organ for the co-ordination of the voluntary movements, or for the excitement of the combined action of muscles.

Some cases of disease of the cerebellum confirm this view; but the majority afford only negative evidence (see Longet, cxxxvi. t. i. p. 742). On the whole, also, it is confirmed by comparative anatomy. The tables of M. Serres show that, although with some exceptions, in the ascending scale of the Vertebrata, the cerebellum undergoes a general increase of size, and acquires an increasing preponderance over the size of the spinal cord, so that we cannot say that its development is unconditionally proportionate to the faculty of combining muscular movements, yet, in each of the four classes of Vertebrata, the species whose natural movements require most frequent and exact combinations of muscular actions are those whose cerebella are most developed in proportion to the spinal cord.

On the strength of all these evidences, the view of M. Flourens has been generally adopted. But M. Foville holds, that the cerebellum is the organ for the perception of muscular sensibility; *i. e.*, of the sensations derived from muscles, through which the mind acquires that knowledge of their actual state and position, which is essential to the exercise of the will upon them. It must be admitted that all the facts

just referred to are as well explained on this hypothesis as on that of the cerebellum being the organ for combining movements; and this hypothesis is, perhaps, more consistent than M. Flourens', with the very close connection between the cerebellum and the posterior columns of the cord.

Gall was led to believe, that the cerebellum is the organ of physical love, or, as Spurzheim called it, of amativeness; and this view is generally received by phrenologists. The facts favouring it are, first, several cases in which atrophy of the testes and loss of sexual passion, have been the consequence of blows over the cerebellum, or wounds of its substance; secondly, cases in which disease of the cerebellum has been attended with almost constant erection of the penis, and frequent seminal emissions; and thirdly, that it has seemed possible to estimate the degree of sexual passion in different persons by an external examination of the region of the cerebellum. With regard to the first class of facts, they are open to the objection that the loss of the sexual passion may have been the consequence of the loss of the testes, and that the latter loss may have been due to some connection in the process of nutrition between the cerebellum and testes, similar to that which exists between the testes and the hair and other parts, whose growth indicates the attainment of puberty, and, for a time, the maintenance of virility. These facts have little bearing on the question, unless it be shown that the loss of sexual passions followed the injury of the cerebellum before the testes began to diminish. The cases of disease of the cerebellum do not prove more; for the same affections of the genital organs are more generally observed in diseases, and in experimental irritations, of the medulla oblongata and upper part of the spinal cord. (See Longet, cxxxvi. t. i. 762).

The facts drawn from craniological examination will receive the credit given to the system of which they are a principal evidence. But, in opposition to them, it must be stated, that there has been a case of complete disorganization or absence of the cerebellum without loss of sexual passion (Combiette, clx.

1831, Longet, and Cruveilhier); that the cocks from whom M. Flourens removed the cerebellum shewed sexual desire, though they were incapable of gratifying it; and that among animals there is no proportion observable between the size of the cerebellum and the development of the sexual passion. On the contrary, many instances may be mentioned in which a larger sexual appetite co-exists with a smaller cerebellum; as *e.g.*, that rays and eels, which are among the fish that copulate, have no laminæ on their almost rudimental cerebella; and that cod-fish, that do not copulate, but deposit their generative fluids in the water, have comparatively well-developed cerebella. Among the Amphibia, the sexual passion is apparently very strong in frogs and toads; yet the cerebellum is only a narrow bar of nervous substance. Among birds there is no enlargement of the cerebellum in the males that are polygamous; the domestic cock's cerebellum is not larger than the hen's, though his sexual passion must be estimated at many times greater than hers. Among Mammalia the same rule holds; and in this class the experiments of M. Lassaigne have plainly shewn, that the abolition of the sexual passion by removal of the testes in early life is not followed by any diminution of the cerebellum; for in mares and stallions the average absolute weight of the cerebellum is 61 grains, and in geldings 70 grains; and its proportionate weight, compared with that of the cerebrum, is, on average, as 1 : 6·59 in mares; as 1 : 5·97 in geldings, and only as 1 : 7·07 in stallions.

On the whole, therefore, it appears advisable to wait for more evidence, before concluding that there is any peculiar and direct connection between the cerebellum and the sexual instinct or sexual passion.* From all that has been observed, no other office is manifest in it than that of regulating and combining muscular movements, or of enabling them to be

* See, on this subject, the report of an interesting discussion at a meeting of the Medico-Chirurgical Society: the Lancet, 1849, vol. i. p. 320.

regulated and combined by so informing the mind of the state and position of the muscles that the will may be definitely and aptly directed to them.

The influence of each half of the cerebellum is directed to muscles on the opposite side of the body; and it would appear that, for the right ordering of movements, the actions of its two halves must be always mutually balanced and adjusted. For if one of its crura, or if the pons on either side of the middle line, be divided, so as to cut off from the medulla oblongata and spinal cord the influence of one of the hemispheres of the cerebellum, strangely disordered movements ensue. The animals fall down on the side opposite to that on which the crus cerebelli has been divided, and then roll over continuously and repeatedly; the rotation being always round the long axis of their bodies, and from the side on which the injury has been inflicted.* The rotations sometimes take place with much rapidity; as often, according to M. Magendie, as sixty times in a minute, and may last for several days. Similar movements have been observed in men; as by M. Serres, in a man in whom there was an apoplectic effusion in the right crus cerebelli; and by M. Belhomme in a woman, in whom an exostosis pressed on the left crus.† They may, perhaps, be explained by assuming that the division or injury of the crus cerebelli produces paralysis, or imperfect and disorderly movements, of the opposite side of the body; the animal falls, and then, struggling with the disordered side on the ground, and striving to rise with the other, pushes itself over; and so, again and

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* Magendie, and Müller, and others following him, say the rotation is *towards* the injured side; but Longet and others more correctly give the statement as in the text. The difference has probably arisen from using the words *right* and *left*, without saying whose right and left are meant, whether those of the observer or those of the observed. When, for example, an animal's right crus cerebelli is divided, he rolls from his own right to his own left, but from the left to the right of one who is standing in front of him.

† See such cases collected and recorded by Dr. Paget (xciv. 1847).

again, with the same act, rotates itself. Such movements cease when the other crus cerebelli is divided; but probably only because the paralysis of the body is thus made almost complete.

### STRUCTURE AND PHYSIOLOGY OF THE CEREBRUM.

The cerebrum is placed in connection with the pons and medulla oblongata by its two *crura* or *peduncles:* it is connected with the cerebellum, by the processes called superior crura of the cerebellum, or *processus a cerebello ad testes*, and by a layer of grey matter, called the valve of Vieussens, which lies between these processes, and extends from the inferior vermiform process of the cerebellum to the corpora quadrigemina of the cerebrum. These parts which thus connect the cerebrum with the other principal divisions of the cerebro-spinal nervous centre form parts of the walls of a cavity (the fourth ventricle) and a canal (the *iter a tertio ad quartum ventriculum*), which are the continuation of the canal that in the fœtus extended through the whole length of the spinal cord and brain. They may therefore be regarded as the continuation of the cerebro-spinal axis or column; on which, as a development from the simple type, the cerebellum is placed; and, on the further continuation of which, structures both larger and more numerous are raised, to form the cerebrum.

The crura cerebri are principally formed of nerve-fibres, of which the inferior are continuous with those of the anterior pyramidal and olivary tracts, and the superior with the round and posterior pyramidal tracts of the medulla oblongata. They may therefore be regarded as, principally, conducting organs; but each of them manifests also the character of a nervous centre, in that it contains a mass of vesicular substance, the *locus niger*, whose nerve-corpuscles abound in pigment-granules and afford some of the best examples of the caudate structure. The office of the crura cerebri as conductors will appear in

speaking of the relation of the cerebrum to voluntary motion, and the peculiar effects of their division: as centres, they are probably connected with the functions of the third nerve, which arises from their inner margins, and through which are directed the chief of the numerous and complicated movements of the eyeball and iris.

On their upper part the crura cerebri bear three pairs of small ganglia, or masses of mingled grey and white nerve-substance, namely, the *corpora geniculata externa*, and *interna*, and the *corpora quadrigemina*, or *nates* and *testes*. Beneath or through the corpora quadrigemina pass the continuations of the round and posterior pyramidal tracts of the medulla oblongata, decussating as they proceed onwards: and nearer to the upper surface of the same ganglia pass the fibres of the superior crura of the cerebellum, mingling with the fibres that form the chief part of the origin of the optic nerves, with the function of which nerves these ganglia appear intimately connected.

In its further course, each crus cerebri, enlarged by the addition of many fibres, forms, as it proceeds, a kind of *fibrous cone*, with its truncated apex in the pons. On it are placed in succession two other ganglia, the optic thalamus and corpus striatum, in which its fibres, and those that are continually added to them, traverse variously-shaped masses and layers of grey substance, and from the anterior part of which, diverging in all directions, and bending backwards, they pass into the substance of the corresponding cerebral hemisphere.

These several organs on each side of the cerebrum are connected by commissures, formed principally of nerve-fibres; namely, the corpora quadrigemina by part of the fibres of the round tract which form the *fillet of Reil*, and meet in the middle line; the optic thalami by the anterior and posterior commissures formed of fibres, and the middle or soft commissure of grey substance; part of the corpora striata and the cerebral hemispheres, by the anterior commissure and corpus callosum. The several parts of each of the hemispheres are also connected

by longitudinal and oblique fibres passing beneath the convolutions from one part to another; and, in the median part of the fornix, connecting the middle cerebral lobe with the optic thalamus.

The cerebral convolutions appear to be formed of nearly parallel plates of fibres, the ends of which are turned towards the surface of the brain, and are overlaid and mingled with successive layers of grey nerve-substance. Some have supposed that the ends of the fibres are connected in loops, of which loops parts are continued from the diverging fibres of the cone, and others from the fibres of the corpus callosum; but this is uncertain. The external grey matter is so arranged in layers, that a vertical section of a convolution generally presents the appearance of three layers of grey, with two intervening layers of white substance, a grey layer being most external. In these grey layers, the outer is formed principally of granular matter and nuclei, like those of nerve corpuscles; in the deeper layer are more perfectly formed cells.*

The *Crura Cerebri* appear as the principal conductors of impressions to and from the cerebrum, and division of one of them produces singular effects on the movements. When one is cut across, the animal moves round and round, rotating round a vertical axis, from the injured towards the sound side, as if from a partial paralysis of the side opposite to the injury. The effect may be supposed due to the interruption of the voluntary impulses from the cerebrum; for even though the cerebellum may have the office of combining the muscles whose co-operation is necessary for each action, yet it is probable that the deliberate effort of the will must proceed from the cerebrum.

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* For further descriptions of the structure of the brain the student should refer to Mayo (clxiii.); Quain (cxlix.); Foville (clxi.); Longet (cxxxvi.); Todd (clix.), or Solly (clxxxviii.). In these works, he will find sufficient guidance to the previous less perfect treatises.

The movements of an animal are more disordered when the cerebellum is removed and the cerebrum is left, that when both cerebrum and cerebellum are removed; as if, in the latter case, the voluntary power were weak but not disordered, but in the former acted with full strength but with disorder.

The *Corpora Quadrigemina* (from which, in function, the *corpora geniculata* are not distinguished), are the homologues of the optic lobes in the birds, Amphibia, and fishes, and may be regarded as the principal nervous centres for the sense of sight. The experiments of Flourens, Longet, and Hertwig, shew that removal of the corpora quadrigemina wholly destroys the power of seeing; and diseases in which they are disorganized are usually accompanied with blindness. Atrophy of them is also often a consequence of atrophy of the eyes.

Destruction of one of the corpora quadrigemina (or of one optic lobe in birds), produces blindness of the opposite eye. The loss of sight thus produced is not only because the corpora quadrigemina contain continuations of the optic tracts, or roots of the optic nerves, but because they are the organs in which the mind perceives the sensations of light. As Longet's experiments shew, when the cerebral hemispheres of a pigeon are removed, and its optic thalami and optic lobes are left, it not only exhibits the reflex movements of the contraction of the iris and the closure of the eyelids when a candle is held to the eye, but when the candle is moved round before the eye, moves its head after it, manifestly because it sees and watches it. It appears, indeed, not to see many things, and runs against obstacles; but this is because, though it may see them, it cannot recognize them, having lost all memory of objects through the loss of its cerebrum.

The loss of sight is the only apparent injury of sensibility sustained by the removal of the corpora quadrigemina. The removal of one of them affects the movements of the body, so that animals rotate, as after division of the crus cerebri, only more slowly: but this is probably due to giddiness and partial

loss of sight. The more evident and direct influence is that produced on the iris. It contracts when the corpora quadrigemina are irritated: it is always dilated when they are removed: so that they may, perhaps, be regarded as the nervous centres governing its movements, and adapting them to the impressions derived from the retina through the optic nerves and tracts.

There is no evidence that the corpora quadrigemina are, in any sense, organs of the intellectual faculties, or of the affections. Yet it may be questioned if their connection with vision be their only function, seeing their large size in fish whose iris is not moveable, and that generally neither their absolute nor their proportionate size in different animals bears any simple relation to the acuteness or extent of their several powers of vision.

The *Optic Thalami* probably participate in a small degree in the visual function of the corpora quadrigemina, for part of the fibres of the optic tract may be traced to their surfaces; and in a recent examination of the brain of a child born without eyes the optic thalami as well as the corpora quadrigemina were found extremely small (cxc. 1851, p. 543). But the results of experiments prove nothing on this point. They only shew disturbances of the power of movement. Irritation of the optic thalami produces no convulsions, and only little pain (Longet and Flourens): destruction of one has effects very similar to those of division of one crus cerebri, namely, a rotation, in which the animal, remaining standing, turns continually round. Schiff, by whom a series of experiments on these various rotations has been made (clxii), has shewn that no such effect follows the removal of any other part of the brain; and Longet points out, as a strong contrast, that after removing all the cerebral hemispheres and the corpora striata, the animal can still stand and walk, but that on removing one of the optic thalami it falls down paralyzed on the opposite side, or commences the rotatory movement. The evidence of apoplexy

and other diseases is similar: all such cases manifest a loss of power of part or the whole of the opposite side of the body.

Concerning the functions of the *Corpora Striata*, experiments, and the effects of diseases, permit none but negative conclusions —such as that they are not the central organs for the sense of smell, nor peculiarly concerned in sensation or movement. The recent experiments of Schiff (clxii.) confirming and, in many respects, correcting those of Magendie and others, shew that when they are removed in rabbits sensation is unimpaired, and the power of movement complete; so that although at first the creature remains at rest, it will, after irritation, or spontaneously, in about half an hour, begin to move, at first slowly, and then with increasing speed and larger leaps, till it strikes against some obstacle, when it falls, and again for a time remains torpid.

Various explanations are offered of these and other strange modes of movements which ensue when the several parts just considered are mutilated, such as that particular masses or tracts in the brain determine the impulses to move in this or that direction, and that, by destroying any part, the balance in which its impulse holds that of the corresponding part of the opposite side is lost. But no such explanations guide to the true physiology of these parts.

Taking together all the parts yet considered, *i.e.*, all the parts of the cerebro-spinal nervous system except the cerebral hemispheres, they appear to include the apparatus, 1st, for the direction and government of all the unfelt and involuntary movements of the parts which they supply; 2nd, for the perception of sensations; and 3rd, for the direction of such instinctive and habitual movements as do not require the exercise of judgment, deliberation, memory, or any other intellectual act. The medulla oblongata and spinal cord have their office in none but involuntary and unconscious movements; but above the medulla oblongata, the pons, and other organs appear capable of such conditions as the mind may perceive, and of being, by the will, excited to the production

of voluntary and orderly movements. But these parts cannot be regarded as organs of the higher faculties of the mind: with them alone, an animal appears to possess neither memory of former sensations, nor judgment to determine and control its actions. Mere sensations, and will, acting according to instinctive impulse and instinctive knowledge or habit, constitute the whole mind of the animal deprived of its cerebral hemispheres.

But seeing what manifestations of mind subsist in animals after the removal of the cerebral hemispheres, it is reasonable to suppose that these lower organs, the *cerebral* or *sensory ganglia*, naturally discharge the functions of which they then appear capable, and that the cerebral hemispheres are engaged in only the higher mental acts. This appears the more probable when it is considered that all the cerebral nerves are in direct connection with these ganglia; and are only through the medium of the highest of them (including herein the olfactory ganglia as part of the brain) connected with the cerebral hemispheres; so that whatever acts are performed through these nerves, independently of the higher faculties of the mind, may be fairly ascribed to the power of these several ganglia. Again the homologues of these organs, that is, of the corpora quadrigemina, the optic thalami, and corpora striata, and the olfactory lobes or ganglia, maintain, in the descending scale of the vertebrate animals a large size, and are proportionate to the development of their organs of sense; while the cerebral hemispheres regularly diminish in their proportion, till in the highest fish they are not larger than these ganglia, and in the lower fish are not so large as the optic or olfactory lobes alone. Now, in the same descending series, the intellectual powers seem to diminish commensurately with the decrease of the cerebral hemispheres; but there is no corresponding decrease of the lower powers of the mind, in the exercise of simple perception and will adapted to the instincts of which these ganglia at the base of the brain are supposed to be the organs.*

* The whole of this subject is well discussed by Dr. Carpenter (ccvii. p. 503 *et seq.*), who regards the "series of ganglionic centres which have

Neither perhaps can any such diminution be traced in those emotions and emotional acts, or expressions, which belong to the instincts that all animals appear to have in common, such as fear, anger, etc.; of these also it is not improbable that the cerebral ganglia may be the organs; but this can only be suspected while we know so little of the emotions to which lower animals are subject.

If it be probable that the functions of the parts already considered are correctly indicated in the preceding paragraphs, it will be in the same degree probable that the functions of the *cerebral hemispheres*, thus determined by "way of exclusion," are those of the organs by which the mind, 1st, perceives those clear and more impressive sensations which it can retain, and judge according to; 2ndly, performs those acts of will each of which requires a deliberate, however quick, determination; 3rdly, retains impressions of sensible things, and reproduces them in subjective sensations and ideas; 4thly, manifests itself in its higher and peculiarly human emotions and feelings, and in its faculties of judgment, understanding,* memory, reflection, induction, and imagination, and others of the like class. The cerebral hemispheres appear thus to be the organs in and through which the mind acts, in all these its operations, which have immediate relation to external and sensible things; and this view may be held without fear, while it is held, also, that

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been enumerated as constituting the real *sensorium*; each ganglion having the power of rendering the mind conscious of the impressions derived from the organ with which it is connected."

* By understanding or intellect is here meant the "faculty of judging according to sense;" a faculty, therefore, which has to do with none but sensible things, and the ideas derived from them. It is often called "reason," or the reasoning faculty; but the term "reason" is here applied only to the higher faculty, which has cognizance of necessary truths and of things above the senses—that which Scripture designates, or includes in the designation, the "Spirit of man."—In the use and adaptation of the terms here employed, the example of Coleridge is followed. See his "Aids to Reflection."

the mind has other and higher parts or faculties, by which it has or may attain to knowledge of things above the senses; namely, the *conscience* and the *pure reason*, which may be instructed otherwise than through the senses, and exercised independently of the brain.

The evidences that the cerebral hemispheres are, in the sense and degree indicated above, the organs of the mind, are chiefly these:—1. That any severe injury of them, such as a general, concussion, or sudden pressure by apoplexy, may instantly deprive a man of all power of manifesting externally any mental faculty. 2. That in the same general proportion as the higher sensuous mental faculties are developed in the vertebrate animals, and in man at different ages, the more is the size of the cerebral hemispheres developed in comparison with the rest of the cerebro-spinal system. 3. That no other part of the nervous system bears a corresponding proportion to the development of the mental faculties. 4. That congenital and other morbid defects of the cerebral hemispheres are, in general, accompanied with corresponding deficiency in the range or power of the intellectual faculties and the higher instincts.

To explain such facts, no hypothesis (if it must be so called while we have regard only to the facts of science) is so sufficient as that which supposes an immaterial principle, not necessarily dependent for its existence on the brain, but incapable of external manifestation, or of knowledge of external things, except through the medium of the brain, and the nervous organs connected therewith. Such a principle would remain itself unchanged, in the case of injury or disease of the brain; but its external manifestations, and all its acts performed in connection with the brain, would be hindered or disturbed; as, for example, the work of any artist might be stopped or spoiled through deficiency or badness of his implements of art. And in the operations of such a principle, it might well be supposed that the power with which its several faculties are manifested would bear a direct proportion to the size of the organs through which they are manifested; for whether we suppose or not

that the principle itself may, in different individuals, have different degrees of power, yet its power of manifestation or perception through the cerebral hemispheres, may vary as those organs do.

But while this may be true respecting those parts of the mind which have to do with the things of sense, it would require much more and different evidence and arguments, to make it probable that the cerebral hemispheres, or any other parts of the brain, are, in any meaning of the term, the *organs* of those parts or powers of the mind which are occupied with things above the senses. The reason or Spirit of man which has knowledge of divine truths, and the conscience, with its natural discernment of moral right and wrong, cannot be proved to have any connection with the brain. In the complex life we live, they are, indeed, often exercised on questions in which the intellect or some other lower mental faculty is also concerned; and in all such cases men's actions are determined as good or bad according to the degree in which they are guided by the higher or by the lower faculties. But the reason and the conscience must be exercised independently of the brain when they are engaged in the contemplation of things which have not been learned through the senses, or through any intellectual consideration of sensible things. All that a man feels in himself, and can observe in others, of the subjects in which his reason and his conscience are most naturally engaged; of the mode in which they are exercised, and the disturbance to which they are liable by the perceptions or ideas of sensible things; of the manner and sources of their instruction; of their natural superiority and supremacy over all the other faculties of the mind; and of his consciousness of responsibility for their use; all teaches him that these faculties are wholly different, not in degree only, nor as different members of one order, but in kind and very nature from all else of which he is composed; all, if rightly considered, must incline him to receive and hold fast the clearer truth which Revelation has given of the nature and destinies of the Spirit to which these, his highest faculties, belong.

Respecting the mode in which the mental principle operates in its connection with the brain, there is no evidence whatever. But it appears that, for all but its highest intellectual acts, one of the cerebral hemispheres is sufficient. For numerous cases are recorded in which no mental defect was observed, although one cerebral hemisphere was so disorganized or atrophied, that it could not be supposed capable of discharging its functions. The remaining hemisphere was, in these cases, adequate to the functions generally discharged by both; but the mind does not seem in any of these cases to have been tested in very high intellectual exercises; so that it is not certain that one hemisphere will suffice for these. In general, the mind combines, as one sensation, the impressions which it derives from one object through both hemispheres, and the ideas to which the two such impressions give rise are single; and in general, also, the mind acts alike in and through both the hemispheres; its actions being, if one may so speak, symmetrical as the hemispheres are. But it would appear that when one hemisphere is disordered, the same object may produce two sensations, and suggest simultaneously different ideas: or, at the same time, two trains of thought may be carried on by the one mind acting, and being acted upon, differently in the two hemispheres. Thus are explicable some of the incoherences of dreaming and delirium; and especially, those singular cases in which a person in delirium, puzzled by the two different, and seemingly simultaneous, trains of thought in which he is engaged, fancies himself two persons, and, as another, holds conversation with himself.*

In relation to common sensation and the effort of the will, the impressions to and from the hemispheres of the brain are carried across the middle line; so that in destruction or com-

* See Dr. Holland's essay on this subject (clxvii.); and Dr. Wigan's essay, and other works, on the Duality of the Mind, or, as it would be better called, of the Brain, for every reasonable person is as conscious of his unity as of his identity; indeed, the idea of personal identity involves that of unity.

pression of either hemisphere, whatever effects are produced in loss of sensation or voluntary motion, are observed on the side of the body opposite to that on which the brain is injured.

In speaking hitherto of the cerebral hemispheres as the organs of the mind, they have been regarded as if they were single organs, of which all parts are equally appropriate for the exercise of each of the mental faculties. But it is a more probable theory, that each faculty has a special portion of the brain appropriated to it as its proper organ. For this theory, the principal evidences among those collected by Drs. Gall and Spurzheim are as follows; 1. That it is in accordance with the physiology of the other compound organs or systems in the body, in which each part has its special function; as, for example, of the digestive system, in which the stomach, liver, and other organs perform each their separate share in the general process of the digestion of the food. 2. That in different individuals, the several mental functions are manifested in very different degrees. Even in early childhood, before education can be imagined to have exercised any influence on the mind, children exhibit various dispositions, each presents some predominant propensity, or evinces a singular aptness in some study or pursuit; and it is a matter of daily observation that every one has his peculiar talent or propensity. But it is difficult to imagine how this could be the case, if the manifestation of each faculty depended on the whole of the brain: different conditions of the whole mass might affect the mind generally, depressing or exalting all its functions in an equal degree, but could not permit one faculty to be strongly and another weakly manifested. 3. The plurality of organs in the brain is supported by the phenomena of some forms of mental derangement, It is not usual for all the mental faculties in an insane person to be equally disordered; it often happens that the strength of some is increased, while that of others is diminished; and in many cases one function only of the mind is deranged, while all the rest are performed in a natural

manner. 4. The same opinion is supported by the fact that the several mental faculties are developed to their greatest strength at different periods of life, some being exercised with great energy in childhood, others only in adult age; and that, as their energy decreases in old age, there is not a gradual and equal diminution of power in all of them at once, but, on the contrary, a diminution in one or more, while others retain their full strength, or even increase in power. 5. The plurality of cerebral organs appears to be indicated by the phenomena of dreams, in which only a part of the mental faculties are at rest or asleep, while the others are awake, and, it is presumed, are exercised through the medium of the parts of the brain appropriated to them. 6. It is stated, that the examination of the brains of individuals, each remarkable for some peculiar propensity or talent, has always demonstrated a corresponding development of a certain portion of the brain.

These facts have been so illustrated and adapted by phrenologists, that the theory of the plurality of organs in the cerebrum thus made probable, has been commonly regarded as peculiar to phrenology, and as so essentially connected with it, that if the system of Gall and Spurzheim be untrue, this theory cannot be maintained. But it is plain that all the system of phrenology built upon the theory may be false, and the theory itself true; for the school of Gall and Spurzheim assume, not only this theory, but also that they have determined all the primitive faculties of which the mind consists, *i. e.*, all the faculties to which special organs must be assigned, and the places of all those organs in the cerebral hemispheres and the cerebellum. Possibly this may be a system of error, founded on a true theory: the cerebrum may have many organs, and the mind as many faculties; but what are the faculties that require separate organs, and where those organs are, may be subjects of which only the first or most general knowledge is yet attained. At any rate, the phrenological physiology of the brain could not be introduced here without

more discussion and objection than is consistent with the plan of this work.*

Of the physiology of the other parts of the brain, little or nothing can be said.

Of the offices of the *corpus callosum*, or great transverse and oblique commissure of the brain, nothing positive is known. But instances in which it was absent, or very deficient, either without any evident mental defect, or with only such as might be ascribed to coincident affections of other parts, make it probable that the office which is commonly assigned to it, of enabling the two sides of the brain to act in concord, is exercised only in the highest acts of which the mind, acting on the brain, is capable. And this view is confirmed by the very late period of its development, and by its absence in all but the placental Mammalia.†

To the fornix and other commissures no special function can be assigned; but it is a reasonable hypothesis that they connect the actions of the parts between which they are severally placed.

As little is known of the functions of the pineal and pituitary glands. Indeed, Osterlen and others raise the question whether either their structure or functions are those of nervous organs, and class them among the glands without ducts (cli.).

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* The phrenological writings of Mr. Combe, and the "Brain and its Physiology," by Mr. Noble, are probably, the best for the medical student who desires to read the arguments in favour of the system. The objections against it may be read in an article in the British and Foreign Medical Review, October, 1846; and in the article *Phrenology*, in the Penny Cyclopædia, from which the above is chiefly taken.

† See cases of congenital deficiency of the corpus callosum, by Mr. Paget and Mr. Henry in the twenty-ninth and thirty-first volumes of the Medico-Chirurgical Transactions.

## PHYSIOLOGY OF THE CEREBRAL AND SPINAL NERVES.

The cerebral nerves are twelve pairs, and the spinal nerves thirty-one pairs, symmetrically arranged on each side of what, reduced to its simplest form, may be regarded as a column or axis of nervous matter, extending from the olfactory bulbs on the ethmoid bone, to the *filum terminale* of the spinal cord in the lumbar and sacral portion of the vertebral canal. The spinal nerves all present certain characters in common, such as their double roots; the isolation of the fibres of sensation in the posterior roots, and those of motion in the anterior roots; the formation of the ganglia on the posterior root; and the subsequent mingling of the fibres in trunks and branches of mixed functions. Similar characters probably belong essentially to the cerebral nerves; but even when one includes the nerves of special sense, it is not possible to discern a conformity of arrangement in any besides the fifth or trifacial, which, from its many analogies to the spinal nerves, Sir Charles Bell designated as the spinal nerve of the head.

According to their several functions, the cerebral or cranial nerves may be thus arranged;—

| | |
|---|---|
| Nerves of special sense . | Olfactory, optic, auditory, part of the glosso-pharyngeal, and the lingual branch of the fifth. |
| „ of common sensation | The greater portion of the fifth, and part of the glosso-pharyngeal. |
| „ of motion . . . . | Third, fourth, lesser division of the fifth, sixth, facial, and hypoglossal. |
| Mixed nerves . . . . | Pneumogastric, and accessory. |

The physiology of the several nerves of the special senses will be considered with the organs of those senses.

## *Physiology of the Third, Fourth, and Sixth Cerebral or Cranial Nerves.*

The physiology of these nerves may be in some degree combined because of their intimate connection with each other in the actions of the muscles of the eye-ball, which they supply. They are probably all formed exclusively of motor fibres: some pain is indicated when the trunk of the third nerve is irritated near its origin; but this may be because of some filaments of the fifth nerve running backwards to the brain in the trunk of the third, or because adjacent sensitive parts are involved in the irritation.

The third nerve, or *motor oculi*, supplies the levator palpebræ superioris muscle, and, of the muscles of the eye-ball, all but the oblique superior or trochlearis, to which the fourth nerve is appropriated, and the rectus externus which receives the sixth nerve. Through the medium of the ophthalmic or lenticular ganglion, of which it forms what is called the short root, it also supplies the motor filaments to the iris.

When the third nerve is irritated within the skull, all those muscles to which it is distributed are convulsed. When it is paralysed or divided, the following effects ensue: first, the upper eye-lid can be no longer raised by the levator palpebræ, but drops and remains gently closed over the eye, under the unbalanced influence of the orbicularis palpebrarum, which is supplied by the facial nerve: secondly, the eye is turned outwards by the unbalanced action of the rectus externus, to which the sixth nerve is appropriated; and hence, from the irregularity of the axes of the eyes, double-sight is often experienced when a single object is within view of both the eyes: thirdly, the eye cannot be moved either upwards, downwards, or inwards; fourthly, the pupil is dilated.

The relation of the third nerve to the iris is of peculiar interest. In ordinary circumstances the contraction of the iris is a reflex action, which may be explained as produced by the

stimulus of light on the retina being conveyed by the optic nerve to the brain (probably to the corpora quadrigemina), and thence reflected through the third nerve to the iris. Hence the iris ceases to act when either the optic or the third nerve is divided or destroyed, or when the corpora quadrigemina are destroyed or much compressed. But when the optic nerve is divided, the contraction of the iris may be excited by irritating that portion of the nerve which is connected with the brain; and when the third nerve is divided, the irritation of its distal portion will still excite contraction of the iris in which its fibres are distributed.

The contraction of the iris thus shews all the character of a reflex act, and in ordinary cases requires the concurrent action of the optic nerve, corpora quadrigemina, and third nerve; and, probably also, considering the peculiarities of its perfect mode of action, the ophthalmic ganglion. But, besides, both irides will contract their pupils under the reflected stimulus of light falling only on one retina or under irritation of one optic nerve. Thus, in amaurosis of one eye, its pupil may contract when the other eye is exposed to a stronger light: and generally the contraction of each of the pupils appears to be in direct proportion to the total quantity of light which stimulates either one or both retinæ, according as one or both eyes are open.

The iris acts also in association with certain other muscles supplied by the third nerve: thus, when the eye is directed inwards, or upwards and inwards, by the action of the third nerve distributed in the rectus internus and rectus superior, the iris contracts, as if under direct voluntary influence. The will cannot, however, act on the iris alone through the third nerve; but this aptness to contract in association with the other muscles supplied by the third, may be sufficient to make it act even in total blindness and insensibility of the retina, whenever these muscles are contracted. The contraction of the pupils when the eyes are moved inwards, as in looking at a near object, has probably the purpose of excluding those

outermost rays of light which would be too far divergent to be refracted to a clear image on the retina; and the dilatation in looking straight forwards, as in looking at a distant object, permits the admission of the largest number of rays, of which none are too divergent to be so refracted.*

The fourth nerve, or *Nervus trochlearis* or *patheticus,* is exclusively motor, and supplies only the trochlearis or obliquus superior muscle of the eyeball. This muscle acts spasmodically when the nerve is irritated, and is paralysed when the nerve is divided or otherwise hindered from its function. From this paralysis results a very slight, if any, deviation of the eye from its normal direction; the pupil is directed a very little upwards and outwards by the unbalanced action of the obliquus inferior, and a peculiar kind of double vision is produced in which the same object appears as two, placed one above the other, but again appears single when the head is inclined towards the shoulder of the opposite side to that on which the superior oblique is paralysed (Szokalski; in Longet, cxxxvi. vol. ii. p. 398). These phenomena are explained by the peculiar actions of the oblique muscles, which as Hunter† shewed (i. vol. iv. p. 274), rotate the eye around its antero-posterior axis, or round such an imaginary line as would nearly correspond with the prolongation of the optic nerve. Thus, when the head is bent down for a certain distance towards either (say the left) shoulder, the corresponding points of the retinæ of both eyes may be held on a level horizontal line by the superior oblique of the right eye rotating the inner part of the eye downwards, and the inferior oblique of the left eye rotating the inner part of its eye upwards. Thus in health, the mind receives a similar and single impression from an object whether the head is erect or turned towards

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* On the contractions of the iris, and the functions of all its nerves, see Dr. Radcliffe Hall's essays (xciv. 1846).

† And more lately, Hueck (clxvi.); Volkmann (xv. art. *Sehen,*); and Dr. G. Johnson (lxxiii. art. *Orbit.*).

either side, through the action of the inferior oblique of one eye being associated with that of the superior oblique of the other. And thus in disease, when one superior oblique is paralysed, the inner half of the retina of that eye is rotated upwards, and when the image of any object falls on it, the mind refers that object to a point lower than that to which it refers the image of the same object on the other retina, though all the inner parts of the latter retina are really lower than the corresponding points of the retina on the paralysed side.

The sixth nerve, *Nervus abducens* or *ocularis externus*, is also, like the fourth, exclusively motor, and supplies only the rectus externus muscle.* The rectus externus is, therefore, convulsed, and the eye is turned outwards, when the sixth nerve is irritated; and the muscle paralysed when the nerve is disorganised, compressed, or divided. In all such cases of paralysis, the eye squints inwards and cannot be moved outwards.

In its course through the cavernous sinus, the sixth nerve forms larger communications with the sympathetic nerve than any other nerve within the cavity of the skull does; and, on this ground, used to be considered as giving origin to the sympathetic. But the import of these communications with the sympathetic, and the subsequent distribution of its filaments after joining the sixth nerve, are quite unknown; and there is no reason to believe that the sixth nerve is, in function, more closely connected with the sympathetic than any other cerebral nerve is.

The question has often suggested itself why the six muscles of the eyeball should be supplied by three motor nerves when

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* In several animals it sends filaments to the iris (Radclyffe Hall); and it has probably done so in man, in some instances in which the iris has not been paralysed, while all the other parts supplied by the third nerve were (see Grant, in Longet, cxxxvi. t. ii. p. 388).

all of them are within reach of the branches of one nerve; and the true explanation would have more interest than attaches to the movements of the eye alone; since it is probable that we have, in this instance, within a small space, an example of some general rule according to which associate or antagonist muscles are supplied with motor nerves.

Now, in the several movements of the eyes we sometimes have to act with symmetrically placed muscles, as when both eyes are turned upwards or downwards, inwards or outwards.* All the symmetrically placed muscles are supplied with symmetrical nerves, *i. e.*, with corresponding branches of the same nerves on the two sides; and the action of these symmetrical muscles is easy and natural, as we have a natural tendency to symmetrical movement in most parts. But because of this tendency to symmetrical movements of muscles supplied by symmetrical nerves, it would appear as if, when the two eyes are to be moved otherwise than symmetrically, the muscles to effect such a movement must be supplied with different nerves. So, when the two eyes are to be turned towards one side, say the right by the action of the rectus externus of the right eye and the rectus internus of the left, it appears as if the tendency to action through the similar branches of corresponding nerves (which would move both eyes inwards or outwards) were corrected, by one of these muscles being supplied by the sixth, and the other by the third nerve. So with the oblique muscles: the simplest and easiest actions would be through branches of the corresponding nerves, acting similarly as symmetrical muscles; but the necessary movements of the two eyes require the contraction of the superior oblique of one side, to be associated with the contraction of the inferior oblique and the relaxation of the superior oblique, of the opposite side. For

* It is sometimes said, that the external recti cannot be put in action simultaneously: yet they are so when the eyes, having been both directed inwards, are restored to the position which they have in looking straight forwards.

this, the fourth nerve of one side is made to act with a branch of the third nerve of the other side; as if thus the tendency to simultaneous action through the similar nerves of the two sides were prevented. At any rate, the rule of distribution of nerves here seems to be, that when, in frequent and necessary movements, any muscle has to act with the antagonist of its fellow on the opposite side, it and its fellow's antagonist are supplied from different nerves.

### *Physiology of the Fifth or Trigeminal Nerve.*

The fifth, trigeminal, or trifacial nerve resembles, as already stated, the spinal nerves, in that its branches are derived through two roots; namely, the *portio major*, the filaments of which expand to receive the corpuscles that form the Casserian ganglion, and the *portio minor*, which has no ganglion, and passes under the ganglion of the portio major to join the third branch or division which issues from it. The first and second divisions of the nerve, which arise wholly from the ganglion of the portio major, are purely sensitive. The third division, which is formed in part by the portio minor, and in part from the Casserian ganglion, is, in its trunk and many of its branches both motor and sensitive.

Through the branches of the greater or ganglionic portion of the fifth nerve, all the anterior and antero-lateral parts of the face and head, with the exception of the skin of the parotid region (which derives branches from the cervical spinal nerves), acquire common sensibility; and among these parts may be included the organs of special sense, from which common sensations are conveyed through the fifth nerve, and their peculiar sensation through their several nerves of special sense. All the muscles, also, acquire muscular sensibility through the filaments of the ganglionic portion of the fifth nerve distributed to them with their proper motor nerves.

Through branches of the lesser or non-ganglionic portion of the fifth the muscles of mastication, namely, the temporal

masseter, two pterygoid, anterior part of the digastric, and mylo-hyoid, derive their motor nerves. The motor function of these branches is proved by the violent contraction of all the muscles of mastication in experimental irritation of the third, or inferior maxillary, division of the nerve; by paralysis of the same muscles, when it is divided or disorganised, or from any reason deprived of power; and by the retention of the power of these muscles, when all those supplied by the facial nerve lose their power through paralysis of that nerve. The last instance proves best, that though the buccinator muscle gives passage to, and receives some filaments from, a buccal branch of the inferior division of the fifth nerve, yet it derives its motor power from the facial, for it is paralysed together with the other muscles that are supplied by the facial, but retains its power when the other muscles of mastication are paralysed. It is probable, therefore, that the buccal branch of the fifth contains only sensitive fibres; and that of these some are supplied to the buccinator muscle, as to all the other muscles some sensitive fibres are distributed to confer muscular sensibility.

The sensitive function of the branches of the greater division of the fifth nerve, if proved by all the usual evidences, such as their distribution in parts that are sensitive and not capable of muscular contraction, the exceeding sensibility of some of these parts, their loss of sensation when the nerve is paralysed or divided, the pain without convulsions produced by morbid or experimental irritation of the trunk or branches of the nerve, and the analogy of this portion of the fifth to the posterior root of the spinal nerve. (See Longet and others.)

But although formed of sensitive filaments exclusively, the branches of the greater or ganglionic portion of the fifth nerve exercise a manifold influence on the movements of the muscles of the head and face, and other parts in which they are distributed. They do so, in the first place, by providing the muscles themselves with that sensibility without which the mind, being unconscious of their position and state, cannot

voluntarily exercise them. It is, probably, for conferring this sensibility on the muscles, that the branches of the fifth nerve communicate so frequently with those of the facial and hypoglossal, and the nerves of the muscles of the eye; and it is because of the loss of this sensibility that when the fifth nerve is divided, animals are always slow and awkward in the movements of the muscles of the face and head, or hold them still, or guide their movements by the sight of the objects towards which they wish to move.

Again, the fifth nerve has an indirect influence on the muscular movements, by conveying sensations of the state and position of the skin and other parts; which the mind perceiving, is enabled to determine appropriate acts. Thus, when the fifth nerve or its infra-orbital branch is divided, the movements of the lips in feeding may cease or be imperfect; a fact which led Sir Charles Bell into one of the very few errors of his physiology of the nerves. He supposed that the motion of the upper lip, in grasping food, depended directly on the infra-orbital nerve; for he found that after he had divided that nerve on both sides in an ass, it no longer seized the food with its lips, but merely pressed them against the ground, and used the tongue for the prehension of the food. Mr. Mayo corrected this error. He found, indeed, that after the infra-orbital nerve had been divided, the animal did not seize its food with the lip, and could not use it well during mastication, but that it could open the lips. He, therefore, justly attributed the phenomena in Sir C. Bell's experiments to the loss of sensation in the lips; the animal not being able to feel the food, and, therefore, although it had the power to seize it, not knowing how or where to use that power.

Lastly, the fifth nerve has an intimate connection with muscular movement through the many reflex acts of muscles of which it is the necessary excitant. Hence, when it is divided, and can no longer convey impressions to the nervous centres to be thence reflected, the irritation of the conjunctiva produces no closure of the eye, the mechanical irritation of the nose

excites no sneezing, that of the tongue no flowing of saliva; and although tears and saliva may flow naturally, their afflux is not increased by the mechanical or chemical or other stimuli, to the indirect or reflected influence of which it is liable in the perfect state of this nerve.

The fifth nerve, through its ciliary branches and the branch which forms the long root of the ciliary or ophthalmic ganglion, exercises, also, some influence on the movements of the iris. When the trunk of the ophthalmic portion is divided, the pupil becomes, according to Valentin (iv. vol. ii. p. 666), contracted in men and rabbits, and dilated in cats and dogs; but, in all cases, becomes immovable, even under all the varieties of the stimulus of light. How the fifth nerve thus affects the iris is unexplained; the same effects are produced by destruction of the superior cervical ganglion of the sympathetic, so that, possibly, they are due to the injury of those filaments of the sympathetic which, after joining the trunk of the fifth, at and beyond the Casserian ganglion, proceed with the branches of its ophthalmic division to the iris; or, as Dr. R. Hall ingeniously suggests, the influence of the fifth nerve on the movements of the iris may be ascribed to the affection of vision in consequence of the disturbed circulation or nutrition in the retina, when the normal influence of the fifth nerve and ciliary ganglion is disturbed. In such disturbance, increased circulation making the retina more irritable might induce extreme contraction of the iris; or, under moderate stimulus of light, producing partial blindness, might induce dilatation: but it does not appear why, if this be the true explanation, the iris should in either case be immovable and unaffected by the various degrees of light.

Furthermore, the complete paralysis or division of the fifth nerve, by the morbid effects which it produces in the organs of special sense, makes it probable that, in the normal state, the fifth nerve exercises some indirect influence on all these organs or their functions. Thus, after such complete paralysis, within a period varying from twenty-four hours to a week, the

cornea begins to be opaque; then it grows completely white; a low destructive inflammatory process ensues in the conjunctiva, sclerotica, and interior parts of the eye; and within one or a few weeks, the whole eye may be quite disorganised, and the cornea may slough or be penetrated by a large ulcer. The sense of smell (and not merely that of mechanical irritation of the nose), may be at the same time lost, or gravely impaired; so may the hearing; and commonly, whenever the fifth nerve is paralysed, the tongue loses the sense of taste in its anterior and lateral parts, *i.e.*, in the portion in which the lingual or gustatory branch of the inferior maxillary division of the fifth is distributed.

The loss of the sense of taste may be due to the lingual branch of the fifth nerve being, really, a nerve of special sense; or it may be because it supplies, in the anterior and lateral parts of the tongue, a necessary condition for the proper nutrition of that part. But, deferring this question until the glossopharyngeal nerve is to be considered, it may be observed that in some brief time after complete paralysis or division of the fifth nerve, the power of all the organs of the special senses may be lost; they may lose not merely their sensibility to common impressions, for which they all depend directly on the fifth nerve, but also their sensibility to the several peculiar impressions for the reception and conduction of which they are purposely constructed and supplied with special nerves besides the fifth. The facts observed in these cases* can, perhaps, be only explained by the influence which the fifth nerve exercises on the nutritive processes in the organs of the special senses. It is not unreasonable to believe, that, in paralysis of the fifth nerve, their tissues may be the seats of such changes as are seen in the laxity, the vascular congestion, œdema, and other affections of the skin of the face and other tegumentary parts which also accompany the paralysis; and that these changes,

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* Two of the best cases are published, with analyses of others, by Mr. Dixon, in the Medico-Chirurgical Transactions, vol. xxviii.

which may appear unimportant when they affect external parts, are sufficient to destroy that refinement of structure by which the organs of the special senses are adapted to their functions.

In the chapter on NUTRITION (p. 306), the question is mentioned whether of the two, the fifth or the sympathetic nerve, conveys the impression by which the nutrition of the parts is influenced; and it is stated that Magendie and Longet have observed, that the destruction of the eye ensues more quickly after division of the trunk of the fifth beyond the Casserian ganglion, or after division of the ophthalmic branch, than after division of the roots of the fifth between the brain and the ganglion. Hence it would appear as if the influence on nutrition were conveyed through the filaments of the sympathetic, which join the branches of the fifth nerve at and beyond the Casserian ganglion, rather than through the filaments of the fifth itself; and this is confirmed by experiments in which extirpation of the superior cervical ganglion of the sympathetic produced the same destructive disease of the eye as commonly follows the division of the fifth nerve.

And yet, that the filaments of the fifth nerve, as well as those of the sympathetic, may conduct such influence appears certain from the cases, including that by Mr. Stanley, in which the source of the paralysis of the fifth nerve was near the brain, or at its very origin, before it receives any communication from the sympathetic nerve. The problem, therefore, cannot yet be certainly solved. The existence of ganglia of the sympathetic in connection with all the principal divisions of the fifth nerve where it gives off those branches which supply the organs of special sense—for example, the connection of the ophthalmic ganglion with the ophthalmic nerve at the origin of the ciliary nerves; of the spheno-palatine ganglion with the superior maxillary division, where it gives its branches to the nose and the palate; of the otic ganglion with the inferior maxillary near the giving off of filaments to the internal ear; and of the sub-maxillary ganglion with the lingual branch of the fifth—

all these connections suggest that a peculiar and probably conjoint influence of the sympathetic and fifth nerves is exercised in the nutrition of the organs of the special senses; and the results of experiment and disease confirm this by showing that the nutrition of the organs may be impaired in consequence of impairment of the power of either of the nerves.

A singular connection between the fifth nerve and the sense of sight, is shown in cases of no unfrequent occurrence, in which blows or other injuries implicating the frontal nerve as it passes over the brow, are followed by total blindness in the corresponding eye. The blindness appears to be the consequence of defective nutrition of the retina; for although, in some cases, it has ensued immediately, as if from concussion of the retina, yet in some it has come on gradually like slowly progressive amaurosis, and in some with inflammatory disorganisation followed by atrophy of the whole eye.* And, again, the fifth nerve is shewn to be intimately connected with the third, by cases in which paralysis of the third has followed neuralgia of the fifth; and not less, by the influence of belladonna applied to the filaments of the fifth, and producing a kind of paralysis of the iris through a reflected narcotising influence on the branches of the third.

## *Physiology of the Facial Nerve.*

The facial, or *portio dura* of the seventh pair of nerves, is the motor nerve of all the muscles of the face, including the platysma, but not including any of the muscles of mastication already enumerated (p. 453); it supplies, also, through the connection of its trunk with the Vidian nerve, by the petrosal nerve, some of the muscles, most probably the levator palati and azygos uvulæ, of the soft palate; by its tympanic branches

* Such a case is recorded by Snabilie in the Nederlandsch Lancet, August, 1846.

it supplies the stapedius and laxator tympani, and through the otic ganglion the tensor tympani; through the *chorda tympani*, it supplies the lingualis and some other muscular fibres of the tongue; and by branches given off before it comes upon the face, it supplies the muscles of the external ear, the posterior part of the digastricus, and the stylo-hyoideus.*

To all these muscles it is the sole motor nerve, and it is probably exclusively motor in its power; no pain is produced by irritating it near its origin, (Valentin), and the indications of pain which are elicited when any of its branches are irritated, may be explained by the abundant communications which, in all parts of its course, it forms with sensitive nerves, whose filaments being mingled with its own are the true source of the pain. Such communications are effected with the fifth nerve through the petrosal nerves, and probably also through the chorda tympani, and with the pneumogastric nerve through its auricular branch, even before the facial leaves the cranium.

When the facial nerve is divided, or in any other way paralysed, the loss of power in the muscles which it supplies, while proving the nature and extent of its functions, displays also the necessity of its perfection for the perfect exercise of all the organs of the special senses. Thus, in paralysis of the facial nerve, the orbicularis palpebrarum being powerless, the eye remains open through the unbalanced action of the levator palpebræ, and the conjunctiva, thus continually exposed to the air and the contact of dust, is liable to repeated inflammation, which may end in thickening and opacity of both its own tissue and that of the cornea. These changes, however, ensue much more slowly than those which follow paralysis of the fifth nerve, and never bear the same destructive character; both because the nutrition of the eye is not directly interfered with, and because the globe can still be moved upwards and

* On the minute anatomy of the facial nerve, see especially Morganti (cxx. 1845, or an abstract in xxv. 1844, p. 53); and Beck (clxiv.).

inwards, so as to carry the cornea partially under the angle of the upper eyelid in winking and sleeping. In paralysis of the facial nerve, also, tears are apt to flow constantly over the face, apparently because of the paralysis of the tensor tarsi muscle, and the loss of the proper direction and form of the orifice of the puncta lacrymalia. By these things the sense of sight is impaired.

The sense of hearing, also, is impaired in many cases of paralysis of the facial nerve; not only in such as are instances of simultaneous disease in the auditory nerves, but in such as may be explained by the loss of power in the muscles of the internal ear. The sense of smell is commonly at the same time impaired through the inability to draw air briskly towards the upper part of the nasal cavities, in which part alone the olfactory nerve is distributed; because, to draw the air perfectly in this direction, the action of the dilators and compressors of the nostrils should be perfect.

Lastly, the sense of taste is impaired, or may be wholly lost, in paralysis of the facial nerve, provided the source of the paralysis be in some part of the nerve between its origin and the giving off of the chorda tympani. This result, which has been observed in many instances of disease of the facial nerve in man, appears explicable only by the influence which through the chorda tympani, it exercises on the movements of the lingualis, and the adjacent muscular fibres of the tongue; and, according to some, or probably in some animals, on the movements of the stylo-glossus. This result is not due to any gustatory fibres conveyed by the chorda tympani from the Vidian nerve to the tongue; for the loss of taste is observed when the facial is paralysed by some affection behind the junction of the petrosal branch of the Vidian, when, therefore, whatever filaments of the Vidian there may be in the chorda tympani, are unaffected. We can, therefore, only suppose that the accurate movement of these muscles in the tongue is essential to the exercise of taste; a fact, if it be so, which is the more singular, because the sense of taste is not

materially impaired in cases of paralysis of all the other muscles of the tongue, through injury of the hypoglossal nerve.

Together with these effects of paralysis of the facial nerve, the muscles of the face being all powerless, the countenance acquires on the paralysed side a characteristic, vacant look, from the absence of all expression: the angle of the mouth is lower, and the paralysed half of the mouth looks longer than that on the other side; the eye has an unmeaning stare. All these peculiarities increase, the longer the paralysis lasts; and their appearance is exaggerated when at any time the muscles of the opposite side of the face are made active in any expression, or in any of their ordinary functions. In an attempt to blow or whistle, one side of the mouth and cheek acts properly, but the other side is motionless or flaps loosely, at the impulse of the expired air; so in trying to suck, one side only of the mouth acts; in feeding, the lip and cheek are powerless, and food lodges between the cheek and gum.

The number of movements concerned in respiration which are performed under the control of the facial nerve, and the great share which it has in the movements most expressive of the states of the mind, led Sir Charles Bell to place the facial in his class of respiratory nerves. But there are no instances in which, when unable to act under ordinary stimuli or in other functions, the facial nerve has yet been capable of action in respiratory movements; its paralysis, when complete, is so in respect to every function alike. As a nerve of expression, it must not be considered independent of the fifth nerve, with which it forms so many communications; for, although it is through the facial nerve alone that all the muscles of the face are put into their naturally expressive actions, yet the power which the mind has of suppressing, controlling and imitating or acting all these expressions, can only be exercised by voluntary and well-educated actions directed through the facial nerve with the guidance of the knowledge of the state and position of every muscle; which knowledge is acquired only through the fifth nerve, which confers sensibility on the muscles, and

appears, for this purpose, to be more abundantly supplied to the muscles of the face than any other sensitive nerve is to those of other parts.

It has been already said, that the facial nerve perhaps supplies the levator palati and azygos uvulæ muscles with motor power; but the same is also ascribed, as probable, to the pneumogastric and accessory nerves. The evidence for the facial is, chiefly, the fact that when it is paralysed, the uvula often deviates to the opposite side, and recovers its medium position when the paralysis ceases; a condition which is also said to be sometimes observed when the petrosal nerves, through which alone the facial can supply the palate, are injured in fracture of the base of the skull. The middle posterior palatine nerve, also, passes into the levator palati and azygos uvulæ, and may, through the petrosal nerve and spheno-palatine ganglion, receive filaments from the facial nerve. But, on the other hand, irritation of the trunk of the facial nerve produces no contractions of these muscles of the palate (Hein, lxxx. 1844; Valentin, iii.); and the experiments of Hein seemed to show that such contractions did follow the irritation of the pneumogastric and accessory nerves, from one or both of which, filaments pass to the palate through branches of the glosso-pharyngeal.*

### *Physiology of the Glosso-Pharyngeal Nerve.*

The glosso-pharyngeal nerves, in the enumeration of the cerebral nerves by numbers according to the position in which they leave the cranium, are considered as divisions of the *eighth pair of nerves*, in which term are included with them the pneumogastric and accessory nerves. But the union of the nerves under one term is inconvenient, although in some parts the glosso-pharyngeal and pneumogastric are so com-

* The several cases relating to this question are given in xxv. 1843-4-5.

bined in their distribution that it is impossible to separate them in either anatomy or physiology.

The glosso-pharyngeal nerve appears to give filaments through its tympanic branch (Jacobson's nerve), to the fenestra ovalis, and fenestra rotunda, and the Eustachian tube; also, to the carotid plexus, and, through the petrosal nerve, to the spheno-palatine ganglion.* After communicating, either within or without the cranium, with the pneumogastric, and, soon after it leaves the cranium, with the sympathetic, digastric branch of the facial, and the accessory nerve, the glosso-pharyngeal nerve parts into the two principal divisions indicated by its name, and supplies the mucous membrane of the posterior and lateral walls of the upper part of the pharynx, the Eustachian tube, the arches of the palate, the tonsils and their mucous membrane, and the tongue as far forwards as the foramen cæcum in the middle line, and to near the tip at the sides and inferior part.

Some experiments make it probable that the glosso-pharyngeal nerve contains, even at its origin, some motor fibres, together with those of common sensation and the sense of taste. For Volkmann (lxxx. 1840), and Hein (lxxx. 1844), when they divided the nerve within the skull, and then irritated its distal portion, saw movements of the pharynx and of the palate and its arches, which appeared to be due to contractions of the stylo-pharyngeus, and, perhaps also, of the palato-glossus muscles. And the recent experiments of Biffi and Morganti (lxxx. 1847, p. 360), confirm these, although their former ones (cxx. 1847) did not. Whatever motor influence, therefore, is conveyed directly through branches of the glosso-pharyngeal may be ascribed to the filaments of the pneumogastric or accessory that are mingled with it.

The experiments of Dr. John Reid (xciv. 1838), confirming those of Panizza and Longet, tend to the same conclusions;

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* See especially Beck (clxiv.).

and their results probably express nearly all the truth regarding the part of the glosso-pharyngeal which is distributed to the pharynx. These results were that,—1. Pain was produced when the nerve, particularly its pharyngeal branches, were irritated. 2. Irritation of the nerve before the origin of its pharyngeal, or of any of these branches, gave rise to extensive muscular motions of the throat and lower part of the face: but, when the nerve was divided, these motions were excited by irritating the upper or cranial portion, while irritation of the lower end, or that in connection with the muscles, was followed by no movement; so that these motions must have depended on a reflex influence transmitted to the muscles through other nerves by the intervention of the nervous centres. 3. When the functions of the brain and medulla oblongata were arrested by poisoning the animal with prussic acid, irritation of the glosso-pharyngeal nerve, before it was joined by any branches of the pneumogastric, gave rise to no movements in the muscles of the pharynx or other parts to which it was distributed; while, on irritating the pharyngeal branch of the pneumogastric, or the glosso-pharyngeal nerve, after it had received the communicating branches just alluded to, vigorous movements of all the pharyngeal muscles and of the upper part of the œsophagus followed.

The most probable conclusion, therefore, may be that what motor influence the glosso-pharyngeal nerve may seem to exercise, is due either to the filaments of the pneumogastric or accessory that are mingled with it, or to impressions conveyed through it to the medulla oblongata, and thence reflected to muscles through motor nerves, especially the pneumogastric, accessory, and facial. Thus, the glosso-pharyngeal nerve excites through the medium of the medulla oblongata the actions of the muscles of deglutition. It is the chief centripetal nerve engaged in these actions; yet not the only one, for, as Dr. John Reid has shewn, the acts are scarcely disturbed or retarded when both the glosso-pharyngeal nerves are divided.

But besides being thus a nerve of common sensation in the parts which it supplies, and a centripetal nerve through which impressions are conveyed to be reflected to the adjacent muscles, the glosso-pharyngeal is also a nerve of special sensation; being the gustatory nerve, or nerve of taste, in all the parts of the tongue to which it is distributed. After many discussions, the question, which is the nerve of taste?—the lingual branch of the fifth, or the glosso-pharyngeal?—may be most probably answered by stating that they are both nerves of this special function. For very numerous experiments and cases have shewn that when the trunk of the fifth nerve or its lingual branch is paralysed or divided, the sense of taste is completely lost in the superior surface of the anterior and lateral parts of the tongue. The loss is instantaneous after division of the nerve; and, therefore, cannot be ascribed to the defective nutrition of the part, though to this, perhaps, may be ascribed the more complete and general loss of the sense of taste when the whole of the fifth nerve has been paralysed.

But, on the other hand, while the loss of taste in the part of the tongue to which the lingual branch of the fifth nerve is distributed proves that to be a gustatory nerve, the fact that the sense of taste is at the same time retained in the posterior and postero-lateral parts of the tongue, and in the soft palate and its anterior arch, to which (and to some parts of which exclusively) the glosso-pharyngeal is distributed, proves that this also must be a gustatory nerve. In a patient in St. Bartholomew's Hospital, the left lingual branch of the fifth nerve was divided in removing a portion of the lower jaw: she lost both common sensation and the sensation of taste in the tip and the anterior parts of the left half of the tongue, but retained both in all the rest of the tongue. M. Lisfranc and others have noted similar cases; and the phenomena in them are so simple and clear, that there can scarcely be any fallacy in the conclusion that the lingual branches of both the fifth and the glosso-pharyngeal nerves are gustatory nerves in the parts of the tongue which they severally supply.

This conclusion is confirmed by some experiments on animals;* and, perhaps, more satisfactorily as concerns the sense of taste in man, by observation of the parts of the tongue and fauces in which the sense is most acute. According to Valentin's experiments made on thirty students, the parts of the tongue from which the clearest sensations of taste are derived, are the base, as far as the foramen cæcum and lines diverging forwards on each side from it; the posterior palatine arches down to the epiglottis; the tonsils and upper part of the pharynx over the root of the tongue. These are the seats of the distribution of the glosso-pharyngeal nerve. The anterior dorsal surface, and parts of the anterior and inferior parts of the tongue, in which the lingual branch of the fifth is alone distributed, conveyed no sense of taste in the majority of the subjects of Valentin's experiments; but even if this were generally the case, it would not invalidate the conclusion that, in those who have the sense of taste in the anterior and upper part of the tongue, the lingual branch of the fifth is the nerve by which it is exercised. And the same may be said of the soft palate and uvula; in those who have the sense of taste in these parts its nerves must be branches of the fifth; for, unless it be through the minute branch which passes into the Jacobsonian plexus, and might thence pass through the superior petrosal nerve and spheno-palatine ganglion, the glosso-pharyngeal nerve can send no filaments to the soft palate.

### *Physiology of the Pneumogastric Nerve.*

The *pneumogastric nerve*, *nervus vagus*, or *par vagum*, has of all the cranial and spinal nerves, the most various distribu-

* Namely, those of Magendie, Mayo, Müller, and Kornfeld (see Müller, xxxii. p. 822); and most completely by those of Dr. Alcock (lxxi. 1836), and of Morganti and Biffi (cxx. 1847). On the contrary are the experiments of Panizzi (recorded by Dr. Burrows, lxxi. vol. xvi.); of Valentin (iii. and iv.), and of Wagner (xxxviii. No. 75). Some explanation of the probable source of the contradiction is given by Morganti (*l. c.*).

tion, and influences the most various functions, either through its own filaments or those which, derived from other nerves, are mingled in its branches.

The parts supplied by the branches of the pneumogastric nerve are as follows; by its pharyngeal branches, which enter the pharyngeal plexus, a large portion of the mucous membrane, and, probably, all the muscles of the pharynx; by the superior laryngeal nerve, the mucous membrane of the under surface of the epiglottis, the glottis, and the greater part of the larynx, and the crico-thyroid muscle; by the inferior laryngeal nerve, the mucous membrane and muscular fibres of the trachea, the lower part of the pharynx and larynx, and all the muscles of the larynx except the crico-thyroid; by œsophageal branches, the mucous membrane and muscular coats of the œsophagus. Moreover, the branches of the pneumogastric nerve form a large portion of the supply of nerves to the heart and the great arteries through the cardiac nerves, derived from both the trunk and the recurrent nerve; to the lungs, through both the anterior and the posterior pulmonary plexuses; and to the stomach by its terminal branches passing over the walls of that organ.

From the parts thus enumerated as receiving nerves from the pneumogastric, it might be assumed that it is a nerve of mixed function, both sensitive and motor. Experiments prove that it is so from its origin, for the irritation of its roots, even within the cranial cavity, produces both pain and convulsive movements of the larynx and pharynx; and when it is divided within the skull, the same movements follow the irritation of the distal portion, shewing that they are not due to reflex action. Similar experiments prove that, through its whole course, it contains both sensitive and motor fibres, but after it has emerged from the skull, and, in some instances even sooner, it enters into so many anastosmoses that it is hard to say whether the filaments it contains are, from their origin, its own, or whether they are derived from other nerves combining with it. This is particularly the case with the filaments of the

sympathetic nerve, which are abundantly added to nearly all the branches of the pneumogastric. The likeness to the sympathetic which it thus acquires, is further increased by its containing many filaments derived, not from the brain, but from its own petrosal ganglia, in which filaments originate, in the same manner as in the ganglia of the sympathetic, so abundantly that the trunk of the nerve is visibly larger below the ganglia than above them (Bidder and Volkmann, xv. art. *Nervenphysiologie*). Next to the sympathetic nerve, that which most importantly communicates with the pneumogastric is the accessory nerve, whose internal branch joins its trunk, and is lost in it.

Properly, therefore, the pneumogastric might be regarded as a triple-mixed nerve; having out of its own sources, motor, sensitive, and sympathetic or ganglionic nerve-fibres; and to this natural complexity it adds that which it derives from the reception of filaments from the sympathetic, accessory, and cervical nerves, and, probably, the glosso-pharyngeal and facial.

The most probable account of the particular functions which the branches of the pneumogastric nerve discharge in the several parts to which they are distributed, may be drawn from Dr. John Reid's experiments on dogs (xciv. vols. xlix. and li.). They show that,—1. The pharyngeal branch is the principal, if not the sole, motor nerve of the pharynx and soft palate,* and is most probably wholly motor; a part of its motor fibres being derived from the internal branch of the accessory nerve. 2. The inferior laryngeal nerve is the motor nerve of the larynx, irritation of it producing vigorous movements of the arytenoid cartilages; while irritation of the superior laryngeal nerve gives rise to no action in any of the muscles attached to the arytenoid cartilages, but merely to contractions of the crico-thyroid muscle. 3. The superior laryngeal nerve is chiefly sensitive;

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* On the probable influence of the facial in the movements of the palate, see p. 462; and on the glosso-pharyngeal, see p. 463.

the inferior, for the most part, motor; for division of the recurrent nerves puts an end to the motions of the glottis, but without lessening the sensibility of the mucous membrane; and division of the superior laryngeal nerves leaves the movements of the glottis unaffected, but deprives it of its sensibility. 4. The motions of the œsophagus are dependent on motor fibres of the pneumogastric, and are probably excited by impressions made upon sensitive fibres of the same; for irritation of its trunk excites motions of the œsophagus, which extend over the cardiac portion of the stomach; and division of the trunk paralyses the œsophagus, which then becomes distended with the food. 5. The cardiac branches of the pneumogastric nerve are one, but not the sole, channel through which the influence of the central organs and of mental emotions is transmitted to the heart. 6. The pulmonary branches form the principal, but not the sole channel by which the impressions on the mucous surface of the lungs that excite respiration, are transmitted to the medulla oblongata. Dr. Reid was unable to determine whether they contain motor fibres; but reasons for believing that they do so, have been already given (p. 157).

From these results, and referring to what has been said in former chapters, the share which the pneumogastric nerve takes in the functions of the several parts to which it sends branches may be understood:—

1. In deglutition, the motions of the pharynx are of the reflex kind. The stimulus of the food, or other substance to be swallowed, acting on the filaments of the glosso-pharyngeal, the filaments of the superior laryngeal given to the pharynx, and the cervical nerves, is conducted to the medulla oblongata, where it is reflected, chiefly through the pneumogastric to the muscles of the pharynx and, perhaps, also of the soft palate (see further, pp. 204 and 422).

2. In the functions of the larynx, the sensitive filaments of the pneumogastric supply that acute sensibility by which the glottis is guarded against the ingress of foreign bodies, or of irrespirable gases. The contact of these stimulates the fila-

ments of the superior laryngeal branch of the pneumogastric; and the impression conveyed to the medulla oblongata, whether it produces sensation or not, is reflected to the filaments of the recurrent or inferior laryngeal branch, and excites contraction of the muscles that close the glottis. Both these branches of the pneumogastric co-operate also in the production and regulation of the voice; the inferior laryngeal determining the contraction of the muscles that vary the tension of the vocal cords, and the superior laryngeal conveying to the mind the sensations of the state of these muscles necessary for their continuous guidance. And both the branches co-operate in the actions of the larynx in the ordinary slight dilatation and contraction of the glottis in the acts of expiration and inspiration, and more evidently in those of coughing and other forcible respiratory movements (p. 174.).

3. It is partly through their influence on the sensibility and muscular movements in the larynx, that the pneumogastric nerves exercise so great an influence on the respiratory process, and that the division of both the nerves is commonly fatal. To determine how death is in these cases, produced has been the object of innumerable, and often contradictory experiments. It is probably produced differently in different cases, and in many is the result of several co-operating causes. Thus, after division of both the nerves, the respiration at once becomes slower, the number of respirations in a given time being commonly diminished to one-half (Emmert, xxxii. p. 371; J. Reid, xciv. 1839; Gilchrist, cxc. Oct. 1858); probably, because the pneumogastric nerves are the principal conductors of the impression of the necessity of breathing to the medulla oblongata. Respiration does not cease; for it is probable, that the impression may be conveyed to the medulla oblongata through the sensitive nerves of all parts in which the imperfectly aerated blood flows (see p. 232); yet the respiration being retarded, adds to the other injurious effects of division of the nerves.

Again, division of both pneumogastric trunks, or of both their recurrent branches, is often very quickly fatal in young

animals; but in old animals, the division of the recurrent nerves is not generally fatal, and that of both the pneumogastric trunks is not always fatal (J. Reid, *l. c.*), and, when it is so, the death ensues slowly. This difference is, probably, because the yielding of the cartilages of the larynx in young animals permits the glottis to be closed by the atmospheric pressure in inspiration, and they are thus quickly suffocated unless tracheotomy is performed (Legallois, cxxxix.). In old animals, the rigidity and prominence of the arytenoid cartilages prevent the glottis from being completely closed by the atmospheric pressure; even when all the muscles are paralysed, a portion at its posterior part remains open, and through this the animal continues to breathe. Yet the diminution of the orifice for respiration may add to the difficulty of maintaining life.

In the case of slower death after division of both the pneumogastric nerves, the lungs are commonly found gorged with blood, œdematous, or nearly solid, or with a kind of low pneumonia, and with their bronchial tubes full of frothy bloody fluid and mucus, changes to which, in general, the death may be proximately ascribed. These changes are due, perhaps in part, to the influence which the pneumogastric nerves exercise on the chemical process of respiration in the lungs, and the movements of the air-cells and bronchi; yet, since they are not always produced in one lung when its pneumogastric nerve is divided, they cannot be ascribed wholly to the suspension or organic nervous influence (J. Reid). Rather, they may be ascribed to the hindrance to the passage of blood through the lungs in consequence of the diminished supply of air, and the excess of carbonic acid in the air-cells (see p. 176): in part, perhaps, to paralysis of the blood-vessels, leading to congestion: and in part, also, as the experiments of Traube especially shew (clxxi. 1846), they appear due to the passage of food and of the various secretions of the mouth and fauces through the glottis, which, being deprived of its sensibility, is no longer stimulated or closed in consequence of their contact. He says,

that if the trachea be divided and separated from the œsophagus, or if only the œsophagus be tied, so that no food or secretion from above can pass down the trachea, no degeneration of the tissue of the lungs will follow the division of the pneumogastric nerves. So that, on the whole, death after division of the pneumogastric nerves may be ascribed, when it occurs quickly in young animals, to suffocation through mechanical closure of the paralysed glottis: and, when it occurs more slowly, to the congestion and pneumonia produced by the diminished supply of air, by paralysis of the blood-vessels, and by the passage of foreign fluids into the bronchi, and aggravated by the diminished frequency of respiration, the insensibility to the diseased state of the lungs, the diminished aperture of the glottis, and the loss of the due nervous influence upon the process of respiration.

4. Respecting the influence of the pneumogastric nerves on the movements of the œsophagus and stomach, the secretion of gastric fluid, the sensation of hunger, absorption of the stomach, and the action of the heart, former pages may be referred to. On all these parts the influence is, as its structure would suggest, like that of the sympathetic more than that of a cerebro-spinal nerve; the movements that follow its irritation being in the stomach slow and continuous, and in the heart rather tardily following the irritation.

### *Physiology of the Accessory Nerve.*

In the preceding pages it is implied that all the motor influence which the pneumogastric nerves exercise, is conveyed through filaments which, from their origin, belong to them: and this is, perhaps, true. Yet a question may still be entertained, which has been often discussed, whether all or a great part of the motor filaments that appear to belong to the

pneumogastric nerves are not given to them from the accessory nerves.*

The principal branch of the accessory nerve, its external branch, supplies the sterno-mastoid and trapezius muscles; and, though pain is produced by irritating it, is composed almost exclusively of motor fibres. It might appear very probable, therefore, that the internal branch, which is added to the trunk of the pneumogastric just before the giving off of the pharyngeal branch is also motor; and that through it the pneumogastric nerve derives part of the motor fibres which it supplies to the muscles enumerated above. And, further, since the pneumogastric nerve has a ganglion just above the part at which the internal branch of the accessory nerve joins its trunk, a close analogy may seem to exist between these two nerves and the spinal nerves with their anterior and posterior roots. In this view, Arnold and several later physiologists have regarded the accessory nerve as constituting a motor root of the vagus nerve; and, although this view cannot now be maintained, yet it is very probable that the accessory nerve gives some motor filaments to the pneumogastric. For, among the experiments on the point, many have shewn that when the accessory nerve is irritated within the skull, convulsive movements ensue in some of the muscles of the larynx; all of which, as already stated, are supplied, apparently, by branches of the pneumogastric: and (which is a very significant fact) Vrolik states that in the chimpansé the internal branch of the accessory does not join the pneumogastric at all, but goes direct to the larynx. On the whole, therefore, although in some of the experiments no movements in the larynx followed irritation of the accessory nerve, yet it may be concluded that it gives to the pneumogastric nerve some of the motor filaments which pass, with the laryngeal branches, to the muscles of the larynx, especially to the crico-thyroid (Bernard, cxxii. 1844).

* An abstract of nearly the whole discussion is given in xxv. 1843-4.

It is not certain whether, besides these, the accessory gives to the pneumogastric any other motor filaments; for the experiments to determine whether, on irritating the accessory within the skull, the muscles of the pharynx, œsophagus, or other parts besides the larynx are convulsed, are completely contradictory, and there appears no other means than that of experiment by which the difficulty may be solved. It is, however, certain that the accessory nerve does not supply *all* the motor filaments which the branches of the pneumogastric contain; for division of the pneumogastric produces a much more extensive paralysis of motion in all the parts that it supplies, than division of the accessory or its internal branch does, especially in regard to the larynx, and other respiratory organs: almost the only effects of destruction of the accessory are loss of voice, and panting in great efforts (Bernard, cxxii. 1844).

Among the roots of the accessory nerve, the lower, arising from the spinal cord, appear to be composed exclusively of motor fibres, and to be destined entirely to the trapezius and sterno-mastoid muscles; the upper fibres, arising from the medulla oblongata, contain many sensitive as well as motor fibres, and these alone are included in the internal branch, which joins the pneumogastric (Bernard, Morganti). Of these, indeed, it is not rare to find some that are united with the pneumogastric at its ganglion, or even within the cranial cavity; and of these upper roots also, the communicating branch is formed, which sometimes takes the place of the posterior root of the first cervical nerve.

As the respiratory nerve, under the influence of the medulla oblongata, the accessory has been often observed to conduct impressions exciting movements necessary to respiration in the sterno-mastoid and trapezius muscles, after these muscles have ceased to move under the influence of the will. They may thus act whenever any of the parts of the brain above the medulla oblongata cease to be capable of conveying impressions; for then the will cannot act on these or any other muscles, though they are still amenable to the reflex influence of the medulla oblongata.

## *Physiology of the Hypoglossal Nerve.*

The hypoglossal, or ninth nerve, or *motor linguæ*, has a peculiar relation to the muscles connected with the hyoid bone, including those of the tongue. It supplies through its descending branch (*descendens noni*), the sterno-hyoid, sterno-thyroid, and omo-hyoid; through a special branch the thyro-hyoid, and through its lingual branches the genio-hyoid, stylo-glossus, hyo-glossus, and genio-hyo-glossus. It contributes, also, to the supply of the submaxillary gland.

The function of the hypoglossal is, perhaps, exclusively, motor. Irritation of it within the the skull produces little if any pain; but since pain is sometimes produced, it may be supposed that the nerve has either some sensitive fibres from its origin, or some which are taking the retrograde course through it to the brain. As a motor nerve, its influence on all the muscles enumerated above is shewn by their convulsions when it is irritated, and by their loss of power when it is paralysed. The effects of the paralysis of one hypoglossal nerve are, however, not very striking in the tongue. Often, in cases of hemiplegia involving the functions of the hypoglossal nerve, it is not possible to observe any deviation in the direction of the protruded tongue; probably because the tongue is so compact and firm that the muscles on either side, their insertion being nearly parallel to the medium line, can push it straight forwards or turn it for some distance towards either side.

The plexus formed between the branches of the descendens noni and those of the second and third cervical nerves serves not only to distribute filaments of the hypoglossal to the depressor muscles of the hyoid bone, but to admit into the descendens noni filaments of the cervical nerves which take a recurrent course through it, and of which some return to the medulla oblongata through the trunk of the hypoglossal, and others go to the tongue through its lingual branches (Volkmann, lxxx. 1840). Hence, and from other connections with

the cervical nerves higher up, the hypoglossal nerve has ample borrowed sensibility.

### *Physiology of the Spinal Nerves.*

Little need be added to what is already said of these nerves (pp. 399 to 401). The anterior roots of the spinal nerves are formed exclusively of motor fibres; the posterior roots exclusively of sensitive fibres.

Beyond the ganglia all the spinal nerves appear to be mixed nerves, and to contain as well sympathetic filaments as those of sensation and motion derived through their own roots.

Of the functions of the ganglia of the spinal nerves nothing very definite is known. That they are not the reflectors of any of the ascertained reflex actions through the spinal nerves, is shewn by the reflex movements ceasing when the posterior roots are divided between the ganglia and the spinal cord.

## PHYSIOLOGY OF THE SYMPATHETIC NERVE.

The sympathetic nerve, or sympathetic system of nerves, obtained its name from the opinion that it is the means through which are effected the several sympathies in morbid action which distant organs manifest. It has also been called *trisplanchnic* nerve, because it is principally distributed among the organs of the three chief visceral systems, the thoracic, abdominal, and pelvic; and the *nervous system of organic life*, in the supposition that it alone, as a nervous system, influences the organic processes. All the terms are defective: for, there is sufficient reason to believe that the cerebro-spinal nervous system may influence the organic functions: the cerebro-spinal system is not excluded from the viscera, nor the trisplanchnic nerve excluded from other parts: the cerebro-spinal system is the medium of numerous sympathies, and the blood of as many or more. But, since the title *sympathetic nerve* has the

advantage of long and most general custom in its favour, and is not more inaccurate than the others, it will be here employed.*

The general differences between the fibres of the cerebro-spinal and sympathetic nerves are already stated (p. 372); and it has been said, that although such general differences exist, and are sufficiently discernible in selected filaments of each system of nerves, yet they are neither so constant, nor of such a kind, as to warrant the supposition, that the different modes of action of the two systems can be referred to the different structures of their fibres. Rather, it is probable, that the laws of conduction by the fibres are in both systems the same, and that the differences manifest in the modes of action of the systems are due to the multiplication and separation of the nervous centres of the sympathetic: ganglia, or nervous centres, being placed in connection with the fibres of the sympathetic in nearly all parts of their course.

In the most general view, the sympathetic system may be described as arranged in two principal divisions, each of which consists of ganglia and connecting fibres. The first division may include the ganglia seated on, or close to, cerebral and spinal nerves, with the filaments issuing from them; the second may comprise the ganglia on the two main branches of the sympathetic, and on its branches in the visceral cavities.

To the first belong the ophthalmic, spheno-palatine, otic, and submaxillary ganglia on the divisions of the fifth nerve; and probably the ganglia on the glosso-pharyngeal and pneumogastric nerves, and on the posterior roots of the spinal nerves; for from all these, fibres appear to originate which, in

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* The title "ganglionic system of nerves," would be in every respect preferable, if it were sure that the ganglia on the spinal nerves give origin to no nerve-filaments but such as are attached to the rest of the ganglionic system, and that no nerve-filaments attached to this system are derived from the brain and spinal cord.

structure, resemble those derived from the proper ganglia of the sympathetic, and are distributed to the same parts. To the second division belong the ganglia arranged in a continuous line along the sides of the vertebræ, with their connecting cords, which make up what have been generally called the trunks of the sympathetic nerve; and all the ganglia placed irregularly on the branches of the sympathetic distributed to the viscera. Of the former the number and proportion correspond generally to the vertebræ; of the latter, to the development of the viscera.

The structure of all these ganglia appears to be essentially similar; all containing, 1st, nerve-fibres traversing them; 2ndly, nerve-fibres originating in them; 3rdly, nerve- or ganglion-corpuscles, giving origin to these fibres; and 4thly, other corpuscles that appear free. And in the trunk, and thence proceeding branches of the sympathetic, there appear to be always, 1st, fibres which arise in its own ganglia; 2ndly, fibres derived from the ganglia of the cerebral and spinal nerves; 3rdly, fibres derived from the brain and spinal cord and transmitted through the roots of their nerves. The spinal cord, indeed, appears to be the principal source of the fibres of the sympathetic nerve.

Respecting the course of the filaments belonging to the sympathetic, the following appears to have been determined. Of the filaments derived from the ganglia on the cerebral nerves, some may pass towards the brain; for, in the trunks of the nerves, between the ganglia and the brain, fine filaments like those of the sympathetic are found. But these may be proceeding from the brain to the ganglia; and on the whole, it is probable that nearly all the filaments originating in the ganglia on cerebral nerves, go out towards the tissues and organs to be supplied, some of them being centrifugal, some centripetal; so that each ganglion with its outgoing filaments may form a kind of special nervous system appropriated to the part in which its filaments are placed. Such, for example, may be the ophthalmic ganglion with the ciliary nerves:

connected with the brain and the rest of the sympathetic system, by the branches of the third, fifth, and sympathetic nerves that form its roots; yet, by filaments of its own, controlling in some mode and degree, the processes in the interior of the eye.

Of the fibres that arise in the spinal ganglia, some appear to pass into the posterior branches of the spinal nerves, and to be distributed with them; the rest pass through the branches by which the spinal nerves communicate with the trunks of the sympathetic, and then entering the sympathetic are distributed with its branches to the viscera. With these, also, a certain number of the large ordinary cerebro-spinal nerve-fibres, after traversing the ganglia, pass into the sympathetic.

Of the fibres derived from the ganglia of the sympathetic itself, some go straightway towards the viscera, the rest pass through the branches of communication between the sympathetic and the anterior branches of the spinal nerves, and joining these spinal nerves, proceed with them to their respective seats of distribution, especially to the more sensitive parts.

Thus, through these communicating branches, which have been generally called roots or origins of the sympathetic nerve, an interchange is effected between all the spinal nerves and the sympathetic trunks; all the ganglia, also, which are seated on the cerebral nerves, have roots (as they are called) through which filaments of the cerebral nerves are added to their own. So that, probably, all sympathetic nerves contain some intermingled cerebral or spinal nerve-fibres; and all cerebral and spinal nerves some filaments derived from the sympathetic system or from ganglia. But the proportions in which these filaments are mingled are not uniform. The nerves of voluntary muscles contain in their trunks a majority of large or cerebro-spinal nerve-fibres, but in their peripheral distribution either only, or a majority of, fine fibres, of which, however, the greater part are of course the cerebro-spinal fibres re-

duced in size. The nerves of the skin, and of most sensitive mucous membranes, contain, for the most part, equal numbers of both large and fine fibres, but the proportions often deviate in both directions; and in all, in their peripheral distribution, the fine fibres greatly preponderate. In the nerves of involuntary muscles, and in those of the less sensitive mucous membranes, there is a great predominance of the fine filaments.*

The physiology of the sympathetic nerve is still very obscure; there are, however, certain statements which may be made in regard to it.

And first, it may be stated generally as nearly certain that the sympathetic nerve-fibres are simple conductors of impressions, as those of the cerebro-spinal system are, and that the ganglionic centres have (each in its appropriate sphere) the like powers both of conducting and of communicating impressions. Their power of conducting impressions is sufficiently proved in ordinary diseases, as when any of the viscera, usually unfelt, gives rise to sensations of pain, or when a part not commonly subject to mental influence is excited or retarded in its actions by the various conditions of the mind; for in all these cases impressions must be conducted to and fro through the whole distance between the part and the spinal cord and brain. So, also, in experiments, now more than sufficiently numerous, irritations of the semilunar ganglia, the splanchnic nerves, the thoracic, hepatic, and other ganglia and nerves, have elicited expressions of

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* For an account of the minute anatomy of the sympathetic nerve, see Kölliker (cxiv. and xv. 1844-5, and ccvi. ccxii. and ccxviii., 1860); Hannover (cxix.); Bidder and Volkmann (cxxvi.); Wagner (cxv.); Remak (clxxii.); Todd and Bowman (xxxix.); Sharpey (cxlix.); Drummond (lxxiii. art. *Sympathetic Nerve*); and the reports in Canstatt's Jahresberichte to 1860.

pain, and have excited movements in the muscular organs supplied from the irritated part.*

In the case of pain excited, or movements affected by the mind, it may be supposed that the conduction of impressions is effected through the cerebro-spinal fibres which are mingled in all, or nearly all, parts of the sympathetic nerves. There are no means of deciding this; but if it be admitted that the conduction is effected through the cerebro-spinal nerve-fibres, then, whether or not they pass uninterruptedly between the brain or spinal cord and the part effected, it must be assumed that their mode of conduction is modified by the ganglia. For, if such cerebro-spinal fibres conducted in the ordinary manner, the parts should be always sensible and liable to the influence of the will, and impressions should be conveyed to and fro instantaneously. But this is not the case; on the contrary, through the branches of the sympathetic nerve and its ganglia none but intense impressions, or impression exaggerated by the morbid excitability of the nerves or ganglia, can be conveyed.

Either, therefore, the nerve-fibres conduct differently in the sympathetic nerves (which is improbable), or else the ganglia have a power of modifying the method of conduction of impressions. It is as if the facility with which an impression may be communicated from one fibre to another in the ganglia were such, that the whole force of ordinary impressions on the nerve-fibres is lost in diffusion among the rest of their contents. This seems not improbable; for some cases shew that when fibres certainly belonging to cerebro-spinal nerves pass through ganglia of, or connected with, the sympathetic, they do not so rapidly, or so surely, transmit impressions as when they have

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* See especially Longet (cxxxvi.); Valentin (iv. vol. ii. p. 107, etc.); Radclyffe Hall (xciv. July, 1846). The last-named observer says, that movements most constantly and actively ensue when the whiter parts of ganglia are irritated; and that they often fail of being produced when the ganglia irritated are grey and pellucid.

no such relation to the ganglia. Thus, the iris is not under the direct or perfect influence of the will; though the passage of filaments of the third nerve to it is shewn by its acting with the muscles supplied by the same nerve. Neither does it always contract when the third nerve is irritated, and when all the other muscles supplied by the same nerve are put in action. So, also, when all the other muscles supplied by the facial nerve contract on irritating its trunk, the levator palati and azygos uvulæ, to which its filaments probably pass through the spheno-palatine ganglion, do not contract.

We may explain these facts, by believing that the impression, whether of the mind, or of artificial irritation, which would be conveyed at once through nerve-fibres, unconnected with ganglia, is, in the ganglia of the sympathetic, communicated and diffused among the corpuscles and the other fibres; and thus, as one may say, is exhausted without reaching the muscles, or, in the case of a centripetal nerve, the spinal cord or brain.

Whether, then, the conduction be effected through proper sympathetic nerve-fibres, or through cerebro-spinal fibres mingled with them and traversing their ganglia, there is this peculiarity to be ascribed either to the fibres or, more probably, to the ganglia — that the conduction is effected more slowly; so that, when, for example, a ganglion on a sympathetic nerve is irritated, the movements in the parts supplied from it, do not immediately ensue, and pain is not indicated till after repeated irritations, or till, by exposure, or otherwise, the fibres and ganglia have become morbidly irritable. But, with this exception, it is probable that the laws of conduction of impressions are the same in both cerebro-spinal and sympathetic systems.

Respecting the general action of the ganglia of the sympathetic nerve little need be said here, since they were taken as examples by which to illustrate the common modes of action of all nervous centres (see p. 389). Indeed, complex as the sympathetic system, taken as a whole, is, it presents in each of its parts a simplicity not to be found in the cerebro-spinal

system: for each ganglion with afferent and efferent nerves forms a simple nervous system, and might serve for the illustration of all the nervous actions with which the mind is unconnected. But it will be more convenient to consider the ganglia now in connection with the functions that they may be supposed to control, in the several organs supplied by the sympathetic system alone, or in conjunction with the cerebro-spinal.

The general processes which the sympathetic appears to influence are those of involuntary motion, secretion, and nutrition.

Many movements take place involuntarily in parts supplied with cerebro-spinal nerves, as the respiratory and other spinal reflex motions; but the parts principally supplied with sympathetic nerves are usually capable of none but involuntary movements, and when the mind acts on them at all, it is only through the strong excitement or depressing influence of some passion, or through some voluntary movement with which the actions of the involuntary part are commonly associated. The heart, stomach, and intestines are examples of these statements; for the heart and stomach, though supplied in large measure from the pneumogastric nerves, yet probably derive through them few filaments except such as have arisen from their ganglia, and are therefore of the nature of sympathetic fibres.

The parts which are supplied with motor power by the sympathetic nerve continue to move, though more feebly than before, when they are separated from their natural connections with the rest of the sympathetic system, and wholly removed from the body. Thus, the heart, after it is taken from the body, continues to beat in Mammalia for one or two minutes, in reptiles and Amphibia for hours; and the peristaltic motions of the intestines continue under the same circumstances. Hence the motion of the parts supplied with nerves from the sympathetic are shewn to be, in a measure, independent of the brain and spinal cord. Their movements, too, though accele-

rated or at least retarded and enfeebled, remain, even after their removal from the body, like those which are natural to them, retaining their character of adaptation to a purpose, and often their harmony and rhythm. They are in all these respects different from the quiverings and twitchings of muscles supplied with cerebro-spinal nerves, when they are similarly separated from the body. The same difference continues when the muscles, having ceased to act spontaneously, are stimulated to fresh contractions by mechanical or other irritation. Of a muscle supplied with cerebro-spinal nerves, only that fasciculus acts to which the stimulus is applied; it instantly twitches once or twice in a disorderly ineffective manner, and then lies at rest again. But of one supplied from the sympathetic nerve, the contraction commences more slowly, but continues longer; it is a more deliberate and more orderly contraction, more like the natural action of the muscle during life, and extending often far beyond the part to which the irritation was first applied. The difference is well shewn (as will be mentioned in the chapter on MOTION) with the electro-galvanic stimulus, and affords a nearly constant and characteristic distinction between the muscles severally supplied by the two nervous systems, and distinguished in their structure by their simple, or their transversely-striated, fibres.

The difference here indicated must, probably, be ascribed to the influence of the ganglia of the sympathetic, which combine for regular and harmonious action the several fasciculi that act in the manner just described. It cannot be ascribed to the nerve-fibres, for all the parts are supplied with a mixture of both cerebro-spinal and ganglionic fibres; and it can hardly be supposed that a peculiar mode of action of the latter could quite counterbalance the tendency to the ordinary action of the former. Neither can the peculiarity be ascribed to the muscular fibres; for the heart has fibres like those of voluntary muscle, yet they act, in this respect, like those of the other muscles supplied with sympathetic nerves and controlled by ganglia.

Among the ganglia, to which this co-ordination of move-

ments is to be ascribed, must be reckoned, not those alone which are on the principal trunks and branches of the sympathetic external to any organ, but those also which lie in the very substance of the organs; such as those discovered in the heart by Remak, others like to which have been found also in the mesentery close by the intestines, in the sub-mucous tissues of the stomach and intestinal canal (Meissner), in the kidneys, and other parts. The extension of discoveries of such ganglia will probably diminish yet further the number of instances in which the involuntary movements appear to be effected independently of central nervous influence.

It seems to be a general rule, at least in animals that have both cerebro-spinal and sympathetic nerves much developed, that the involuntary movements excited by stimuli conveyed through ganglia are orderly and like natural movements, while those excited through nerves without ganglia are convulsive and disorderly; and the probability is that, in the natural state, it is through the same ganglia that natural stimuli, impressing centripetal nerves are reflected through centrifugal nerves to the involuntary muscles. As the muscles of respiration are maintained in uniform rhythmic action chiefly by the reflecting and combining power of the medulla oblongata, so, probably, are those of the heart, stomach, and intestines, by their several ganglia. And as with the ganglia of the sympathetic and their nerves, so with the medulla oblongata and its nerves distributed to respiratory muscles,—if these nerves or the medulla oblongata itself be directly stimulated, the movements that follow are convulsive and disorderly; but if the medulla be stimulated through a centripetal nerve, as when cold is applied to the skin, then the impressions are reflected so as to produce movements which, though they may be very quick and almost convulsive, are yet combined in the plan of the proper respiratory acts.

Such, then, seems to be the peculiarity of the action of the sympathetic nerve, and especially of its ganglia, in determining the involuntary movements of the parts that it supplies. And, as first stated, this peculiarity seems to be due, not to an

essentially different mode of action in either the fibres or the ganglia of the sympathetic, but to the arrangement of those ganglia, which are inserted in or very near to the parts whose movements they control.

Respecting the influence of the sympathetic nerve in nutrition and secretion, we may refer to the chapters on those processes (pp. 303 to 306, and pp. 328-9). The mode in which this influence is exercised is still obscure, though probably it is in a great measure connected with the supply of blood to the parts. The experiments of Bernard, Waller, Brown-Séquard, and others, render certain that the sympathetic nerve possesses great influence over the contractile power of the blood-vessels, division of the trunk or branch of such nerve being followed by paralysis of the coats of the vessels supplied by the ramifications of the divided nerve, and by consequent congestion and increased temperature of the parts in which such vessels are distributed; while galvanic or other stimulus to the nerve is followed by contrary effects, namely by contraction of the vessels and diminution in the quantity of blood and in temperature. So constant and important are these results, that the sympathetic nerve may be regarded as having, for its principal office the power of regulating and controlling the supply of blood to parts, its fibres constituting the true vasomotor nerves. Besides acting directly upon the coats of the vessels and thus determining the supply of blood, the sympathetic appears also to influence the nutritive and secretory changes in a part by direct action on its tissue, whereby it is stimulated to increased activity of function; for the changes in the mode of nutrition and secretion in a part cannot be altogether explained by mere variations in the diameter of its blood-vessels, or in the quantity of blood supplied to it. Daily observation shews multiform results in secretion and nutrition in cases of disease, of which all have, for a common condition, the enlargement of the blood vessels of the diseased part; something, therefore, besides the enlargement of the

vessels, must in these cases determine the different events: and so when the various exercise of nervous influence in a part affects the size of its vessels and the supply of blood, this change cannot be considered as the only source of the change in its mode of secretion or nutrition.

Important though the influence of the sympathetic is, over the processes of nutrition and secretion, yet it seems nearly certain that much of this influence is derived from the cerebro-spinal nervous centres, from which the majority of the sympathetic nerve-fibres arise. This is especially shown in regard to the nervous influence regulating the contraction and dilatation of blood-vessels, whereby the supply of blood to parts is so largely determined; injury or division of any part of the cord being followed by dilatation of vessels supplied by nerves issuing from the neighbourhood of the injured part, while contraction of the vessels ensues on galvanic or other irritation of the cord or the trunks of its nerves.

It is, of course, very difficult to determine the relative share exercised by the true sympathetic and the ordinary cerebro-spinal fibres in the contraction of blood-vessels, and in the general processes of nutrition and secretion, since both kinds of fibres appear to be distributed to most parts, and there seems to be no possibility of isolating them. The difficulty of determining this point is much greater in the higher than in the lower Vertebrata; for it would appear that, in the same proportion as the centres of the cerebro-spinal system are developed, so is its connection with the processes of organic life more intimate. In frogs, for instance, all the organic functions may be carried on for several days after the removal of the brain and spinal cord, saving only the medulla oblongata for the maintenance of respiration; but in Mammalia, and, most of all, in man, even a slight injury of either brain or spinal cord may disturb all the organic functions. The regular movements of the stomach and intestines, the heart, and urinary bladder, independently of the spinal cord or brain, is manifested by numerous experiments in reptiles

and Amphibia; but in Mammalia, the separation of these organs from the spinal cord or brain, is sufficient to render their actions feeble and irregular, or, after a time, to stop them altogether.

Probably, therefore, the safest view of the question at present is, still to regard all the processes of organic life, in man, as liable to the combined influences of the cerebro-spinal and the sympathetic systems; to consider that those influences may be so combined as that the sympathetic nerves and ganglia may be in man, as in the lower animals, the parts through which the ordinary and constant influence of the nervous force is exercised on the organic processes; while the cerebro-spinal nervous centres and their ganglia are the parts from which the proper sympathetic ganglia may derive supplies of nervous force, and from which, more often or more regularly than in the lower animals, the processes of the organic and the animal life are made to work in connection and mutual adaptation.*

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## CHAPTER XVI.

### CAUSES AND PHENOMENA OF MOTION.

THE vital motions of the solid parts of animals present two principal kinds, differing in the organs of their production, in

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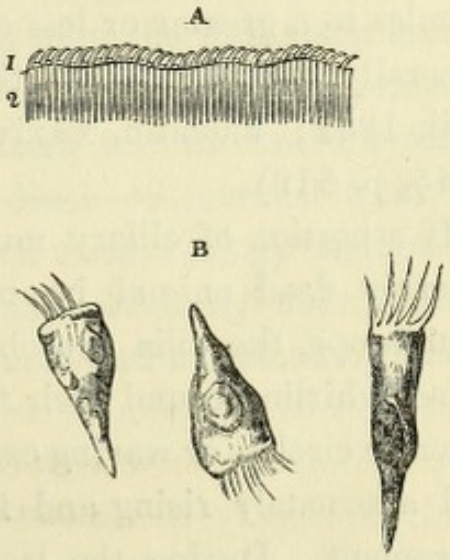
* For a succinct analysis of most of our present knowledge on the functions of the sympathetic nerve, especially in relation to nutrition and secretion, the reader is referred to Dr. Brown Séquard's important lectures, in the *Lancet*, 1858 (especially Lect. 9 and 10); also, for valuable details, to M. Bernard's lectures, now being published in the *Medical Times and Gazette*, 1860), the researches of Professor Lister (xliii. 1857), and Dr. H. F. Campbell (ccxxxvi.); and to an interesting paper by Dr. J. W. Ogle, in the 41st vol. of the *Medico-Chirurgical Transactions*.

their phenomena, and in their causes: they are first, the oscillatory motion or vibration of microscopic cilia, with which the surfaces of certain membranes are beset; and secondly, the motion from contraction of fibres, which either have a longitudinal direction and are fixed at both extremities, or form circular bands: the contraction or shortening of the fibres bringing the fixed parts nearer to each other.

### CILIARY MOTION.

As just said, this consists in the incessant vibration of fine, pellucid, blunt processes, about $\frac{1}{3000}$th of an inch long, termed cilia, situated on the free extremities of the cells of epithelium covering certain surfaces of the body. The form of epithelium on which cilia occur is most commonly of the cylindrical kind (fig. 49; see also p. 320); but sometimes, as on the surface lining the cerebral ventricles, it is of the tesselated variety.

*Fig.* 49.*




In man, and probably in Mammalia generally, the ciliary epithelium lines the interior of the nasal cavity, except the olfactory region (Todd and Bowman, xxxix. vol. ii. p. 5), and of the frontal and other sinuses communicating with it, the lachrymal canal and sac, and is spread over the mucous surface of both eyelids, but not over the conjunctiva covering the eye

* Fig. 49. A. Cilia, as seen vibrating on a portion of the mucous membrane of the trachea of a rabbit; 1, the cilia; 2, lines indicating the several epithelial cells on which the cilia are placed. After Valentin. B. Separate cylinders of epithelium with cilia attached, from the trachea of the cat. After Henle.

itself. From the posterior part of the nasal cavity, it passes to the upper part of the pharynx, which it lines to about opposite the lower border of the atlas: it is also spread over the upper surface of the soft palate, and laterally is continued to the orifice of the Eustachian tube, through which canal it extends into the cavity and membrane of the tympanum. Ciliary epithelium occurs also over the whole extent of the respiratory mucous tract, commencing at the larynx, and ceasing only near the terminations of the bronchi (pp. 146-7). It is met with also in the female generative apparatus, commencing about the neck of the uterus, extending along the Fallopian tubes to their fimbriated extremities, and continued for a short distance along the peritoneal surfaces of the tubes; and in the male it occurs in the epididymis (Hassall). In Mammalia there is no instance of its occupying any part of the urinary mucous surface; but in reptiles it lines the urinary tubules to a greater or less extent, and sometimes, though not generally, proceeds within the Malphigian capsules (Bowman, xliii. 1842; Valentin, xxxiv. bd. viii. p. 92; Kölliker, lxxx. 1845, p. 519).

If a portion of ciliary mucous membrane from a living or recently dead animal be moistened, and examined with a microscope, the cilia are observed to be in constant motion, either whirling round their fixed extremities so that their ends describe circles, or waving continually backwards and forwards, and alternately rising and falling with a lashing or fanning movement. During the lashing movements each of the cilia performs a motion somewhat similar to that performed during the feathering of an oar in rowing (Quekett, lxxi. May, 1844): hence the general result of their movements is to produce a continuous current in a determinate direction; and this direction is invariably the same on the same surface, being usually towards its external orifice. In the production of such current probably consists the principal use of the cilia, which are thus enabled to propel the fluids or minute particles which come within the range of their influence, and to aid in their expul-

sion from the body. In the Fallopian tube the direction of the current excited by the cilia is towards the cavity of the uterus, and may thus be of service in aiding the passage of the ovum. Of the purposes served by the cilia covering the surface of the cerebral ventricles nothing is known.

The nature of the ciliary motion, and the cause on which it depends, are equally obscure. It seems to be alike independent of the will, of the direct influence of the nervous system, and of muscular contraction; for it is involuntary, there is no nervous or muscular tissue in the immediate neighbourhood of the cilia, and it continues for several hours after death or removal from the body, provided the portion of examined tissue is kept moist. Its independence of the nervous system is shewn also in its occurrence in the lowest invertebrated animals apparently unprovided with anything analogous to a nervous system, in its persistence in animals killed by prussic acid, narcotic or other poisons, and after the direct application of narcotics to the ciliary surface, or the discharge of a Leyden jar, or of a galvanic shock through it. In their rhythmic action and its persistence after death or removal from the body, the ciliary movements bear a close analogy to those of the heart: and the analogy is made closer by both kinds of movements being diminished by cold and increased by heat.*

## MUSCULAR MOTION.

Muscular tissue is of two chief kinds, usually distinguished by structural peculiarities and mode of action. The first kind includes the muscles of organic life, which (with the exception of the fibres of the heart, the lymphatic hearts of birds and reptiles, and the stomach and intestines of some fish), consist of simple, smooth filaments; the second comprises the muscles

* For the best accounts of Cilia, see Dr. Sharpey (lxxiii. art. *Cilia*) and Henle (xxxvii.).

of animal life, and the heart, and other exceptions just named which consist of compound and apparently striated fibres, or tubes including fibres. The difference, however, between these two kinds of muscular tissue is less marked than used to be supposed; for both in structure and mode of action they often closely resemble each other. See especially Ellis (xliii. 1859), and Kölliker (ccxviii. p. 63).

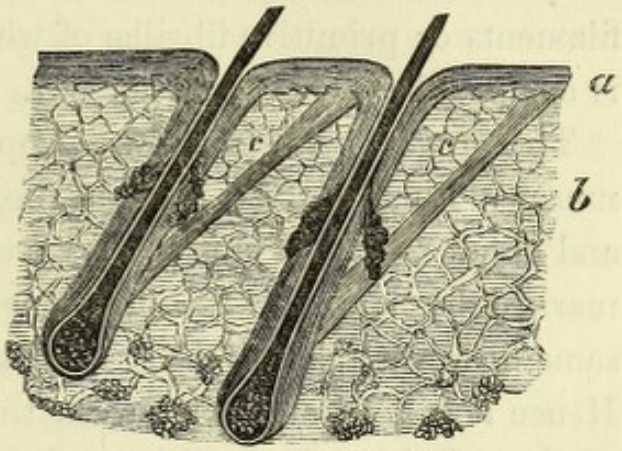
The *muscles of organic life*, or *unstriped muscles* as they are also called, consist of fibres, or, according to Kölliker, of elongated spindle-shaped fibre-cells, which in their most perfect form are flat, from $\frac{1}{4700}$ to $\frac{1}{3100}$ of an inch broad, very clear, granular, and brittle, so that when they break, they often have abruptly rounded or square extremities. Some of them are uniform; many bear nuclei; many are marked along the middle, or, more rarely, along one of the edges, either by a fine continuous dark streak, or by short isolated dark lines, or by dark points arranged in a row, or scattered. Fibres such as these are collected in divers numbers in fasciculi, upon which the dark lines just mentioned sometimes form, by branches which they give off and receive, a sort of network, and sometimes run tortuously (pl. ii. fig. 9).

Fibres of organic muscles, such as are here described form the proper contractile coats of the digestive canal from the middle of the œsophagus to the external sphincter ani, of the ureters and urinary bladder, the trachea and bronchi, the ducts of glands, the gall-bladder, the vesiculæ seminales, the pregnant uterus, and the arteries.

This form of tissue also enters largely into the composition of the tunica dartos, and is the principal cause of the wrinkling and contraction of the scrotum on exposure to cold: the fibres of the cremaster assist in some measure in producing this effect, but are chiefly concerned in drawing up the testis and its coverings towards the inguinal opening. It occurs largely also in the cutis, being especially abundant at the interspaces between the bases of the papillæ. Hence, when it contracts under the influence of cold, fear, electricity, or any other

stimulus, the papillæ are made unusually prominent, and give rise to the peculiar roughness of the skin termed *cutis anserina*, or gooseskin. It occurs also in the superficial portion of the cutis, in all parts where hairs occur, in the form of flattened roundish bundles, which lie alongside the hair-follicles and sebaceous glands. They pass obliquely from without inwards, embrace the sebaceous glands, and are attached to the hair-follicles near their base (Fig. 50.) Fibres of this tissue, also, constitute part of the walls of most gland-ducts and lymphatics, and are the chief agents concerned in the propulsion of the contents of these canals.

*Fig.* 50.*




The *muscles of animal life*, or *striped muscles*, include the whole class of voluntary muscles, the heart, the muscular tissue of the pharynx and upper part of the œsophagus, the lymphatic hearts of birds and reptiles, and the stomach and intestines of some fish. The voluntary muscles are composed of fleshy bundles inclosed in coverings of fibro-cellular tissue, by which each is at once connected with, and isolated from, those adjacent to it. Each bundle is again divided into smaller ones, similarly ensheathed and similarly divisible; and so on, through an uncertain number of gradations, till, just beyond the reach of the unaided eye, one arrives at the *primitive fasciculi*, or the *muscular fibres* peculiarly so called.

The *primitive fasciculi* consist of tubes of delicate structureless membrane, the *sarcolemma* of Mr. Bowman, inclosing a number of filaments. They are cylindriform or prismatic, with five or more sides, according to the manner in which they are

Fig. 50. Perpendicular section through the scalp, with two hair-sacs; *a* Epidermis; *b* cutis; *c* muscles of the hair-follicles (after Kölliker, ccxviii.).

compressed by adjacent fasciculi. Their breadth varies in different animals, from $\frac{1}{600}$ to $\frac{1}{3000}$ of an inch; in man from $\frac{1}{2000}$ to $\frac{1}{3000}$, the average of the majority being about $\frac{1}{4000}$. Their most striking, though not constant, characteristics, are their pale yellow colour, and their being apparently marked by striæ, which pass transversely round them, in slightly curved or wavy parallel lines, from $\frac{1}{10000}$ to $\frac{1}{12000}$ of an inch apart. Other, but generally more obscure striæ, also pass longitudinally over the tubes, and indicate the size and direction of the filaments or primitive fibrillæ of which the primitive fasciculus is composed (pl. ii. figs. 7 and 8).

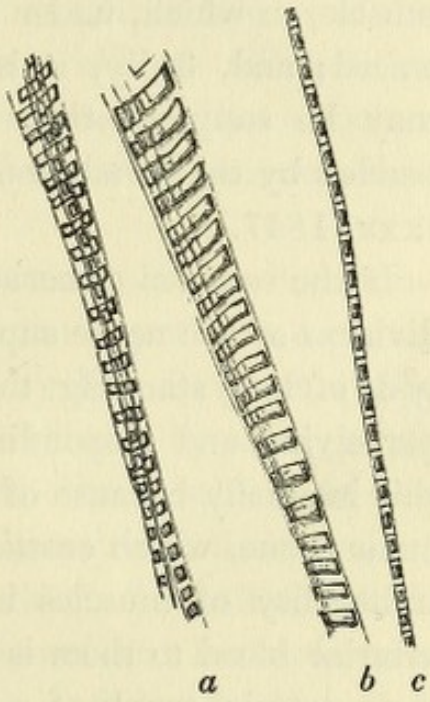
The *primitive fibrils* are the proper contractile tissue of the muscle. Each of them is cylindriform, but somewhat flattened, and about $\frac{1}{18000}$ of an inch its greatest thickness. They are marked by transverse impressions, which are at exactly the same distance apart as the striæ on the surface of the fasciculus. Hence it is generally concluded, that the striated appearance of the primitive fasciculi is produced by the filament being so apposed, that the transverse marks on all those near the surface lie at exactly the same levels.

Each primitive fasciculus contains several hundreds of the primitive fibrils; and when fully formed they fill all the cavity of the sarcolemma, with the exception of very small interspaces, which seem occupied with a glutinous pellucid fluid, It is only in immature fasciculi that there is an appearance of a central cavity, which is filled either with fluid or with minute granules.

At present, there is much question of the true structure of the fibrils, and of the source of their seeming constrictions, or transverse impressions. Some deny the existence of such constrictions, except when the muscle is contracted, or in some particular condition after death; while others believe that the fibrils are rows of corpuscles, or discs, connected by a homogenous transparent substance. The transverse marks on the fibrils, and the ordinary striæ on the fasciculus, correspond to the spaces between the discs. The most recent view on the

subject is that published almost simultaneously by Dr. Sharpey (cxlix.) and Dr. Carpenter, (cl.), according to which the alternate dark and light particles, of which the fibril is composed, have each a quadrilateral, and generally a rectangular form. Every bright particle or space is marked across its centre by a fine, dark, transverse line or shadow, by which the space is divided into two equal parts; and sometimes a bright border may be perceived on either side of the fibril, so that each of the rectangular dark bodies appears to be surrounded with a bright area, having a similar quadrangular outline, as if the pellucid substance inclosed it on all sides (see fig. 51). These appearances would seem to show that the elementary particles of which the fibril is made up, are little masses of pellucid substance, possibly nucleated cells, presenting a rectangular outline, and appearing dark in the centre.

*Fig.* 51.*




*Properties of Muscular Tissue.*

The property of muscular tissue, by which its peculiar functions are exercised, is its contractility, through which the

* Fig. 51. Muscular fibrils of the pig, magnified 720 diameters. *a.* An apparently single fibril, shewing the quadrangular outline of the component particles, their dark central part and bright margin, and their lines of a junction crossing the light intervals. *b.* A longitudinal segment of a fibre, consisting of a number of fibrils still connected together. The dark cross stripes and light intervals on *b* are obviously occasioned by the dark specks and intervening light spaces respectively corresponding in the different fibrils. *c.* Other small collections of fibrils. From a preparation by Mr. Lealand. After Dr. Sharpey.

contraction or shortening of muscle is excited by all kinds of stimuli, applied either directly to the muscles, or indirectly to them through the medium of their motor nerves. This property, although commonly brought into action through the nervous system, appears to be inherent in the muscular tissue, and not derived by it from the nerves (see p. 32). For 1st., it may be manifested in a muscle which is isolated from the influence of the nervous system by division of the nerves supplying it, so long as the natural tissue of the muscle is duly maintained by nutrition; 2ndly, it is manifest in a portion of muscle, in which, under the microscope, no nerve-fibre can be traced; and, 3rdly, it is retained in all the muscles when it may be supposed that the function of their nerves is suspended by the inhalation of ether or of chloroform (Harless, lxxx. 1847.).

If the removal of nervous influence is long continued, as by division of the nerve supplying a muscle, or in cases of paralysis of long standing, the irritability, *i. e.*, the power of both perceiving and responding to a stimulus, may be lost; but this is chiefly because of the impaired nutrition of the muscular tissue, which ensues through its inaction (J. Reid). The irritability of muscles is also soon lost, unless a supply of arterial blood to them is kept up. Thus, after ligature of the main arterial trunk of a limb, the power of moving the muscles is partially or wholly lost, until the collateral circulation is established; and when, in animals, the abdominal aorta is tied, the hind legs are rendered almost powerless (Segalas, xxxii. p. 895.) So, also, it is to the imperfect supply of arterial blood to the muscular tissue of the heart that the cessation of the action of this organ in asphyxia is in some measure due (page 76).

Besides the property of contractility, the muscles, especially those of animal life and striated, possess sensibility by means of the sensitive nerve-fibres distributed to them. The amount of common sensibility in muscles is not great; for they may be cut or pricked without giving rise to severe pain, at least

in their healthy condition. But they have a peculiar sensibility, or at least a peculiar modification of common sensibility, which is shown in that their nerves can communicate to the mind an accurate knowledge of their states and positions when in action. By this sensibility, we are not only made conscious of the morbid sensations of fatigue and cramp in muscles, but acquire, through muscular action, a knowledge of the distance of bodies and their relation to each other, and are enabled to estimate and compare their weight and resistance by the effort of which we are conscious in measuring, moving, or raising them. Except with such knowledge of the position and state of each muscle, we could not tell how or when to move it for any required action; nor without such a sensation of effort could we maintain the muscles in contraction for any prolonged exertion.

The *mode of contraction* in the transversely-striated muscular tissue, has been much disputed. The most probable account, which has been especially illustrated by Mr. Bowman (xliii. 1840-1841), is that the contraction is effected by an approximation of the constituent parts of the fibrils, which, at the instant of contraction, without any alteration in their general direction, become closer, flatter, and wider; a condition which is rendered evident by the approximation of the transverse striæ seen on the surface of the fasciculus, and by its increased breadth and thickness. The appearance of the zigzag lines into which it was supposed the fibres are thrown, in contraction, is due to the relaxation of a fibre which has been recently contracted, and is not at once stretched again by some antagonist fibre, or whose extremities are kept close together by the contractions of other fibres. The contraction is therefore a simple, and, according to Ed. Weber, an uniform, simultaneous, and steady shortening of each fibre and its contents. What each fibril or fibre loses in length, it gains in thickness: the contraction is a change of form, not of size; it is, therefore, not attended with any diminution in bulk from condensation of the tissue. This has been proved for entire muscles, by

making a mass of muscle, or many fibres together, contract in a vessel full of water, with which a fine, perpendicular, graduated tube communicates. Any diminution of the bulk of the contracting muscle would be attended by a fall of fluid in the tube; but when the experiment is carefully performed, the level of the water in the tube remains the same, whether the muscle be contracted or not (Barzelotti; Mayo, xxxii. p. 886; Valentin, iv., Matteucci, cxxiv.).*

In thus shortening, muscles appear to swell up, becoming rounder, more prominent, harder, and apparently tougher. But this hardness of muscle in the state of contraction, is not due to increased firmness or condensation of the muscular tissue, but to the increased tension to which the fibres, as well as their tendons and other tissues, are subjected from the resistance ordinarily opposed to their contraction. When no resistance is offered, as when a muscle is cut off from its tendon, not only is no hardness perceived during contraction, but the muscular tissue is even softer, more extensile, and less elastic than in its ordinary uncontracted state. (Ed. Weber, xv. art. *Muskelbewegung*).

*Heat* is *developed* in the contraction of muscles. Becquerel and Breschet found with the thermo-multiplier, about 1° of heat produced by each forcible contraction of a man's biceps; and when the actions were long continued, the temperature of the muscle increased 2°. It is not known whether this development of heat is due to chemical changes ensuing in the muscle, or to the friction of its fibres vigorously acting: in either case, we may refer to it a part of the heat developed in active exercise, especially by the lower animals. And Nasse suspects that to it is due the higher temperature of the blood in the left ventricle; for he says it is always warmer in the left ventricle than in the left auricle, and that the blood in

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* Edward Weber, however, states that a very slight diminution does take place in the bulk of a contracting muscle; but it is so slight as to be practically of no moment.

the latter is but little warmer than that on the right side of the heart. But these experiments need confirmation.

*Sound* is said to be *produced* when muscles contract forcibly. Dr. Wollaston showed that this sound might be easily heard by placing the tip of the little finger in the ear, and then making some muscles contract, as those of the ball of the thumb, whose sound may be conducted to the ear through the substance of the hand and finger. A low shaking or rumbling sound is heard, the height and loudness of the note being in direct proportion to the force and quickness of the muscular action, and the number of fibres that act together, or, as it were, in time.

In the smooth, or simple muscular fibres, scarcely any of the phenomena just described have been observed. The fibres are believed to contract with a simple shortening, but the exact mode, and the phenomena attending it, have not been satisfactorily determined.

The two kinds of fibres have characteristic differences in the mode in which they act on the application of the same stimulus; differences which may perhaps be ascribed more to their respective modes of connection with the nervous system than to their structures (see p. 483). When irritation is applied directly to a muscle with striated fibres, or to the motor nerve supplying it, contraction of the part irritated, and of that only, ensues; and this contraction is instantaneous, and ceases on the instant of withdrawing the irritation. But when any part with smooth-fibre muscles, *e. g.*, the intestines, or bladder, or a duct is irritated, the subsequent contraction ensues more slowly, extends beyond the part irritated, and, with alternating relaxations, continues for some time after the withdrawal of the irritation. Ed. Weber (xv. art. *Muskelbewegung*) has particularly illustrated the difference in the modes of contraction of the two kinds of muscular fibres by the effects of the electro-magnetic stimulus. The rapidly succeeding shocks, given by this means to the nerves of muscles, excite in all the transversely striated muscles a fixed state of tetanic contrac-

tion, which lasts as long as the stimulus is continued, and on its withdrawal instantly ceases: but in the muscles with smooth fibres they excite, if any movement, only one that ensues slowly, is comparatively slight, alternates with rest, and continues for a time after the stimulus is withdrawn.

In their mode of responding to these stimuli, all the voluntary muscles, or those with transverse striæ, are alike; but among those with simple fibres there are many differences,—a fact which tends to confirm the opinion, that their peculiarity depends as much or more on their connection with nerves and ganglia, than on their own properties. According to Weber, the ureters and gall-bladder are the parts least excited by stimuli: they do not act at all till the stimulus has been long applied, and then contract feebly, and to a small extent. The contractions of the cæcum and stomach are quicker and wider spread: still quicker those of the iris, and of the urinary bladder if it be not too full. The actions of the small and large intestines, the vas deferens, and pregnant uterus are yet more vivid, more regular, and more sustained; and they require no more stimulus than that of the air to excite them. The heart is the quickest and most vigorous of all the muscles of organic life in contracting upon irritation, and appears in this, as in nearly all other respects, like the connecting member of the two classes of muscles.

All the muscles retain their property of contracting under the influence of stimuli applied to them, or to their nerves, for some time after death, the period being longer in cold-blooded than in warm-blooded Vertebrata, and shorter in birds than in Mammalia. It would seem as if the more active the respiratory process in the living animal, the shorter is the time of duration of the irritability in the muscles after death; and this is confirmed by the comparison of different species in the same order of Vertebrata. But the period during which this irritability lasts, is not the same in all persons, nor in all the muscles of the same persons. In man it ceases, according to Nysten, in the following order:—first, in the left ventricle,

then in the intestines and stomach, the urinary bladder, right ventricle, œsophagus, iris; then in the voluntary muscles of the trunk, lower and upper extremities; lastly in the left and right auricle of the heart.

After the muscles of the dead body have lost their irritability or capability of being excited to contraction by the appliration of a stimulus, they spontaneously pass into a state of contraction, apparently identical with that which ensues during life.* It affects all the muscles of the body; and, where external circumstances do not prevent it, commonly fixes the limbs in that which is their natural posture of equilibrium or rest. Hence, and from the simultaneous contraction of all the muscles of the trunk, is produced a general stiffening of the body, constituting the *rigor mortis* or *post-mortem rigidity*.

The muscles are not affected exactly simultaneously by the post-mortem contraction, but rather in succession. It affects the neck and lower jaw first; next, the upper extremities, extending from above downwards; and lastly reaches the lower limbs; in some rare instances only, it affects the lower extremities before, or simultaneously with, the upper extremities. It usually ceases in the order in which it began; first at the head, then in the upper extremities, and, lastly, in the lower extremities. According to Sommer, it never commences earlier than ten minutes, and never later than seven hours, after death; and its duration is greater in proportion to the lateness of its accession.

Since the rigidity does not ensue until muscles have lost the capacity of being excited by external stimuli, it follows that all circumstances which cause a speedy exhaustion of muscular irritability, induce an early occurrence of the rigidity, while conditions by which the disappearance of the irritability is

* If, however, arterial blood be made to circulate through the body or through a limb, the contraction of the muscles thus supplied with blood, may, according to Brown-Séquard, be suspended, and the muscles again admit of contracting on the application of a stimulus (cxc. Oct. 1851, p. 542; and cci.).

delayed, are succeeded by a tardy onset of this rigidity. Hence its speedy occurrence and equally speedy departure in the bodies of persons exhausted by chronic diseases; and its tardy onset and long continuance after sudden death from acute diseases. In some cases of sudden death from lightning, violent injuries, or paroxysms of passion, the rigor mortis appears not to occur at all; but this is not always the case. (See lxxi. May 16, 1851.) It may, indeed, be doubted whether there is really a complete absence of the post-mortem rigidity in any such cases; for the experiments of M. Brown-Séquard with electro-magnetism, make it probable that the rigidity may supervene immediately after death, and then pass away with such rapidity as to be scarcely observable. Thus he took five rabbits, and killed them by removing their hearts. In the first, rigidity came on in 10 hours, and lasted 192 hours; in the second, which was feebly electrified, it commenced in seven hours, and lasted 144; in the third, which was more strongly electrified, it came on in two, and lasted 72 hours; in the fourth, which was still more strongly electrified, it came on in one hour, and lasted 20; while in the last rabbit, which was submitted to a powerful electro-galvanic current, the rigidity ensued in seven minutes after death, and passed away in 25 minutes. From this it appears that the more powerful the electric current, the sooner does the rigidity ensue, and the shorter is its duration; and as the lightning-shock is so much more powerful than any ordinary electric discharge, the rigidity may ensue so early after death and pass away so rapidly as to escape detection. The influence exercised upon the onset and duration of post-mortem rigidity by causes which exhaust the irritability of the muscles was well illustrated in further experiments by the same physiologist, in which he found that the rigor mortis ensued far more rapidly and lasted for a shorter period, in those muscles which had been powerfully electrified just before death, than in those which had not been thus acted upon (cxix. 1849).

The occurrence of rigor mortis is not prevented by the previous existence of paralysis in a part, provided the paralysis has not been attended with very imperfect nutrition of the muscular tissue.

The rigidity affects the involuntary as well as the voluntary muscles, whether they be constructed of striped or unstriped fibres. The rigidity of involuntary muscles with striped fibres is shewn in the contraction of the heart after death (p. 77), when it constitutes what has been called concentric hypertrophy. The contraction of the muscles with unstriped fibres is shewn by an experiment of Valentin (iv. Bd. ii. p. 36), who found that if a graduated tube be connected with a portion of intestine taken from a recently-slain animal, filled with water and tied at the opposite end, the water will in a few hours rise to a considerable height in the tube, owing to the contraction of the intestinal walls. It is still better shewn in the arteries, of which all that have muscular coats contract after death, and thus present the roundness and cord-like feel of the arteries of a limb lately removed, or a body recently dead. Subsequently they relax, as do all the other muscles, and feel lax and flabby, and lie as if flattened, and with their walls nearly in contact.*

*Actions of Muscles.*—The simplest division of muscular actions, and one which, for practical use, is most convenient, is into the voluntary and involuntary actions. But it is comparatively useless and uninstructive in the consideration of the general physiology of muscular movements; for, as we have seen, the structure of muscles does not exactly correspond with their having habitually the voluntary or the involuntary mode of action; neither can any muscles be said, unconditionally, to be either voluntary, or involuntary, since many in-

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* Several interesting points in relation to post-mortem rigidity may be found in the late Mr. W. F. Barlow's papers on Muscular Contractions after Death from Cholera (lxxi. 1849-50): and much information on the physiology of muscular action in the writings of Dr. C. B. Radcliffe (ccxxix.).

voluntary movements are performed by muscles subject to the will, and many muscles that are commonly independent of the will are liable to be affected by it or other acts of the mind. More than all, whether a muscle is involuntary or not depends not on itself, but on the nervous system; for, if the brain be removed or inactive, all the muscles become involuntary ones.

Neglecting, therefore, this distinction, it will be more instructive to follow Müller in an enumeration of the modes in which movements may be excited, either in single muscles, or in groups of muscles combined for united or opposite actions.

1. The first class of movements may be named *automatic*, the parts seeming to "have in themselves the power of motion,"* and not only the power, but the mode and plan.

These may include all those muscular actions which are not dependent on the will or any other act of the mind; which are either persistent, or periodical with a regular rhythm; and are dependent on normal natural causes seated in the nerves or the central organs of the nervous system. The cause of the rhythmic movements may be, as has been shewn, either in the sympathetic or the cerebro-spinal nervous centres, but never in nerve-fibres. Of the automatic movements dependent chiefly on the sympathetic, the principal are those of the heart, the intestinal canal, uterus, and urinary bladder. The automatic movements of the heart are nearly like those of the animal muscles, quick, and succeeding each other quickly; those of the other organs are more gradual and more enduring, and their intervals of rest are much longer. Whether this difference be owing to the different structure of the muscle, or to the nature of the nervous influence, has been already considered but not decided.

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* Those which Müller names "movements excited by heterogeneous stimuli," are here omitted, because of the doubt whether any such occur naturally.

It is a characteristic of the automatic movements of all the viscera of organic life, that a certain order of succession is observed in the contractions; one part of the viscus contracts before another, and the motion thus traverses the organ in a determinate direction during each period of the rhythm. In the heart, the motion commences in the venæ cavæ, and proceeds through the auricles and ventricles, and then, after an interval, is resumed in the venæ cavæ (p. 76). In the intestine, the movement travels in a vermicular manner from above downwards; and a second movement, beginning at the upper part of the intestine before the first has completed its course, affects the parts in the same order. The action of stimuli on those organs endowed with automatic motion does not generally alter the order of the contractions, unless it be excessive and abnormal; but it influences the rapidity and force of the contractions; thus stimuli, whether external or internal, acting on the heart, cause it to beat more quickly and forcibly, and motions of the intestinal canal are rendered both more rapid and energetic by external irritation, as when the intestine is exposed to the air; or by internal irritation of its mucous membrane, as in diarrhœa. Such irritation, also, may proceed from the nervous centres; so disorder of the spinal cord may produce spasmodic automatic movements of the intestinal canal and uterus: and irritation of the cœliac ganglion may accelerate the movements of the intestines, but generally, in all these cases, the natural mode, *i.e.*, the plan and order of the movements is maintained.

As already stated, the constant and primary cause of the rhythmic contractions of these and of all the organic muscles is probably connected with the mode of action of the sympathetic nerve and its ganglia. Their continuance, when the organs are removed from the body, proves that they do not depend on the brain or spinal cord; and their purposive and orderly character indicates that they are directed through nervous centres, such as are found only in the sympathetic system. The supposed mode of action of the sympathetic

ganglia in determining such movements is stated at pp. 96, 268, etc.

But there are also automatic movements which are dependent on the central organs of the cerebro-spinal nervous system. Such are the involuntary movements of respiration, the nervous centre governing which, appears to be in the medulla oblongata. These have been sufficiently considered (pp. 174, 420). Such also are the motions of the muscles of the eye and of the iris during sleep, in which the eye is generally turned somewhat inwards and upwards, and the iris is contracted, although light is excluded; and such, probably, is the normal and habitual winking of the eye-lids, for the purpose apparently of maintaining the moisture of the conjunctiva.

All these movements have some kind of time or rhythm. Other automatic movements controlled by the cerebro-spinal centres are persistent: such as those of the sphincters. For, although we have voluntary power over these muscles to strengthen their contraction, yet their action continues independently of volition, during sleep as well as in the waking state, and it cannot be voluntarily interrupted, except by exerting a counter pressure against it by their antagonist muscles. The principal sphincter among the animal muscles is the sphincter ani, the force and impulse to the contraction of which are derived from the spinal cord (p. 407), from which a constant motor impulse seems to be directed to it.

2. The second class of muscular movements may be named *antagonistic* movements. There are groups of muscles opposed to each other in their action in almost all parts of the body. The extremities have flexors and extensors, supinators and pronators, abductors and adductors, and rotators inwards and rotators outwards. When the muscles of one lateral half of the face are paralysed, those of the opposite half of it draw the features towards their side. The tongue, when one half of it is paralysed, may be drawn to the opposite side. Hence it would appear that the muscular fibres, especially those of

animal life, are constantly in a state of slight contraction; and that the state of inaction of the different parts of our body does not indicate an absolutely relaxed condition of the muscles, but rather that the different groups of muscles antagonise and balance each other; and that when the position of a part is changed from the medium state of apparent rest, one or more of the muscles, already in a state of antagonistic action, are merely thrown into more powerful contraction.

When muscles have few or no antagonists, they always tend to give to the parts on which they act a determinate position. Thus there are numerous muscles which rotate the thigh outwards, while the rotation inwards can be effected but feebly by the tensor vaginæ femoris. Hence arises the involuntary tendency to the turning outwards of the whole limb in walking, sitting, or lying. The sphincters are also muscles which have no proper antagonists. The constant occlusion of the orifices of the viscera by the sphincters can be accounted for, therefore, by the fact of the contraction of muscles not wholly ceasing in the state of apparent rest, and of their having no antagonising muscles; without its being necessary to suppose that a constant current of nervous influence is transmitted specially to them.

3. *Reflex Movements.*—The character of the reflected movements has been already explained (pp. 393, etc.). They include all muscular actions which arise from impressions on centripetal nerves exciting motor nerves to action through the intervention of the nervous centres; and arrange themselves into two principal groups, of which the first may include the reflex movements determined by the brain and spinal cord.

4. Of the *Associate or Consensual Movements*, the peculiarity consists in the voluntary impulse to one motion giving rise to the production of other motions contrary to, or independently of, the will; thus, whenever the eye is voluntarily directed inwards, the iris contracts. The less perfect the action of the nervous system, the more frequently do associate

movements occur. It is only by education that we acquire the power of confining the influence of volition, in the production of voluntary motions, to a certain number of nervous fibres issuing from the brain. An awkward person, in performing one voluntary movement, makes many movements, which are produced involuntarily by consensual nervous action. In the piano-forte player we have an example, on the other hand, of the faculty of insulation of the nervous influence in its highest perfection. The motions most prone to be associated involuntarily are those of the corresponding parts of the two sides of the body: as the motions of the irides, of the muscles of the ear, of the eye-lids, and of the extremities in the attempt to effect opposed motions. Some of the most remarkable facts illustrating the association and antagonism of muscular actions are presented by the muscles which move the eyes (pp. 451-2).

The organic muscles also are, in some measure, subject to the laws of association. The increased frequency and force of the heart's action during muscular exertions of the body, are probably, in some measure, owing to this cause. The action of the voluntary muscles has an influence on that of the intestinal canal, and on that of the urinary bladder. Every one is aware how beneficial muscular exercise is in preserving the regularity of the muscular action of the intestines, and the regularity of excretion.

5. Of the *movements dependent on certain states of the mind*, there are three classes: those dependent on mere ideas passing through the mind; those arising from the passions, emotions, or affections; and those which are voluntary movements.

Certain groups of muscles of the animal system are in a constant state of proneness to involuntary motion, owing to the susceptibility of their nerves, or rather of the parts of the brain from which they arise, to be excited by ideas. Thus all the respiratory muscles, including those supplied by the facial nerve, may be excited to action merely by particular states of the mind. Any sudden change in the state of the mind, a

sudden change of thought such as occurs when the idea of the ridiculous arises in the mind, without any passion being excited, is capable of giving rise to a corresponding action of the nerves, evidenced in the muscles of the face and the respiratory muscles. Yawning, inasmuch as it can be excited by the mere idea, or by seeing or hearing another yawn, belongs to the same class of movements. The disposition to the movements of the features and the respiratory muscles that constitute laughing and yawning, exists previously and is manifested when the idea gives to the nervous force the determinate direction. Ideas of fearful or detestable objects suddenly excited, even when called up by mere fictions, occasion, in persons of excitable temperament, the motion of shuddering; and the same occurs, sometimes, from the mere thought of a disgusting medicine: vomiting, indeed, may be produced by the mere recollection of a disagreeable taste.

It is, again, principally the respiratory portion of the nervous system which is involuntarily excited to the production of muscular actions by the passions and emotions of the mind. The change in the state of the brain seems to be propagated to the medulla oblongata, which causes a change of action in the respiratory muscles, through the medium of their nerves, including the facial nerve, which is pre-eminently the nerve of expression.

The exciting passions give rise to spasms, and frequently even to convulsive motions, affecting the muscles supplied by the respiratory and facial nerves. Not only are the features distorted, but the actions of the respiratory muscles are so changed as to produce the movements of crying, sighing, and sobbing. During the sway of depressing passions, such as fear, or terror, all the muscles of the body become relaxed,—the motor influence of the brain and spinal cord being depressed. The feet will not support the body, the features hang as without life, the eye is fixed, the look is completely vacant, and void of expression, the voice feeble or extinct. Frequently the state of the feelings, under the influence of passion, is of a

mixed character; the mind is unable to free itself from the depressing idea; yet the effort to conquer this gives rise to an exciting action in the brain. In these mixed passions, the expression of relaxation in certain muscles,—in the face, for example — may be combined with the active state of others; so that the features are distorted, whether in consequence merely of the antagonising action of the opposite muscles being paralysed, or by a really convulsive contraction. Disorderly as the mode in which these emotional influences are exercised may seem to be, yet to each emotion certain combined movements are appropriated, and become *expressive* of it. The nerves of certain groups of muscles seem to be naturally combined to act together when the appropriate emotion is felt, as the respiratory nerves are for the common respiratory movements. Like these movements, also, the emotional movements may be controlled by the will, though essentially independent of it, and though, when the stimulus exciting them is very strong, they may occur in opposition to the effort of the will. With these actions of the muscles of animal life, those of organic life are often associated; the disturbed action of the heart during mental emotions is an instance of such association.

Of the *voluntary movements* we have already spoken in connection with the physiology of the motor nerves and the brain. In all the former instances, we are scarcely, or not at all, conscious of the movements that take place, or are only conscious of them by other senses than the muscular sense, as by seeing the movement. And this may be connected with the probability that the central organs determining these movements are not the organs in which the mind can either clearly discern sensations, or deliberately exercise the will (see p. 438). In the voluntary motions we have both consciousness and intention; though not in all cases an equal degree of either, for in movements habitually performed we are hardly either conscious or intent.

We have no knowledge of how the will acts in the brain,

through which alone its full influence can be directed to the nerves (see p. 441); but the influence of the will on the motor fibres is not a solitary fact of its kind. Through the brain we have the power of voluntarily directing the mind to all the cerebral and spinal nerves, even to the nerves of common sensation, and the nerves of special sense; we exercise this power whenever we *attend* to sensations. If two persons are addressing different words to our opposite ears, we can by attention follow what is said by the one, while we leave what the other says unnoticed. The same circumstance is observed in the case of simultaneous impressions on different senses. According to the direction in which we give our attention, we cease to see distinctly while we exert the power of hearing to a greater degree, and *vice versâ;* for only one object at a time can be taken cognizance of by the faculty of attention (see p. 383). Thus, we have the power of directing the attention according to our will; the will has here the same influence as in the production of voluntary motions. The only difference is, that in the latter case the motor nerve-fibres, previously in a state of repose, are excited to action; while in attending to the impressions on the sensitive nerves, the action of the will consists in rendering the sensation more intense or distinct. Neither is the power of the will limited to the motor and sensitive nerves; it also influences the mental operations; we have the power of voluntarily directing our thoughts. In short, we see that the voluntary effort of the mind can be directed upon motor or sensitive nerves, or made to affect the mental operations; an act of volition is nothing else than the voluntary and conscious direction of the nervous forces in the brain upon different cerebral apparatus; and on the part of the brain subjected to this voluntary action of the nervous principle, it depends, whether the effect shall be a muscular movement, a more distinct perception, or an idea connected with some sensible object.

As a general rule, a voluntary movement is more difficult the smaller the number of nervous fibres required to be excited,

and the smaller the part to be moved. The nervous force more readily excites many than few nervous fibres to action; hence the tendency to the associate movements described at page 507. It is doubtful whether distinct portions of a long muscle can be voluntarily excited to independent and separate action. The action of the nervous force is therefore less capable of localization when excited by volition than when determined by accidental involuntary stimuli. From external causes very small parts of a muscle, for example, of the biceps of the arm, are seen to contract separately; but this never occurs from voluntary influence. The power of confining the voluntary excitement of the nervous principle to distinct groups of fibres is increased by much exercise, and the more frequently certain groups of fibres are excited to action by the influence of the will, the more capable do they become of isolated action; this is exemplified in performers on the piano-forte, etc.

Motions very frequently performed occur at last whenever the nervous influence in the brain receives, in the slightest degree, the direction necessary to produce them; as if the conducting power of the nervous fibres, and the combining power of the nervous centres, increased with the frequency of their excitement. Hence the facility of the habitual movements; hence the mimic movements of the hands in speaking; and thus obscure ideas, without any distinct consciousness, often give rise to determinate and appropriate motions, provided these motions have been previously many times excited in the same manner; the effort of the will in producing these movements being as obscurely felt as the sensation or idea that led to them.

# CHAPTER XVII.

## OF VOICE AND SPEECH.

In nearly all air-breathing vertebrate animals there are arrangements for the production of sound, or *voice*, in some part of the respiratory apparatus. In many animals, the sound admits of being variously modified and altered during and after its production; and, in man, one of the results of such modification is *speech*.

### *Mode of Production of the Human Voice.*

It has been proved, by observations on living subjects, as well as by experiments on the larynx taken from the dead body, that the sound of the human voice is the result of the inferior laryngeal ligaments, or vocal cords, which bound the glottis, being thrown into vibrations by currents of expired air impelled over their edges. Thus, if a free opening exists in the trachea, the sound of the voice ceases, but returns on the opening being closed. An opening into the air-passages above the glottis, on the contrary, does not prevent the voice being formed. M. Magendie, also, has shewn that the voice is not lost, though the epiglottis, the superior ligaments of the larynx, and the upper part of the arytenoid cartilages be injured. The same may be observed in cases of disease; and in injuries, when the vocal cords are exposed, they may be seen vibrating during the emission of sound. Injury of the laryngeal nerves supplying the muscles which move the vocal cords puts an end to the formation of vocal sounds; and when these nerves are divided on both sides, the loss of voice is complete. Moreover, by forcing a current of air through the larynx in the dead subject clear vocal sounds are produced, though the epiglottis, the upper ligaments of the larynx, the ventricles

between them and the inferior or vocal ligaments, and the upper part of the arytenoid cartilages, be all removed; provided the vocal cords remain entire, with their points of attachment, and are kept tense and so approximated that the fissure of the glottis may be narrow.

The vocal ligaments, therefore, may be regarded as the proper organs of the mere voice : the modifications of the voice are effected by other parts as well as by them. Their structure is adapted to enable them to vibrate like tense membranes, for they contain a large quantity of elastic tissue ; and they

*Fig.* 52.*

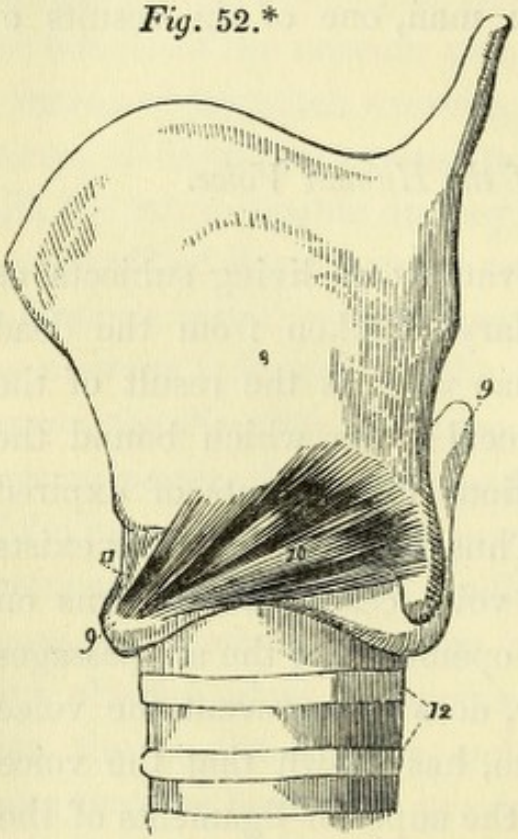
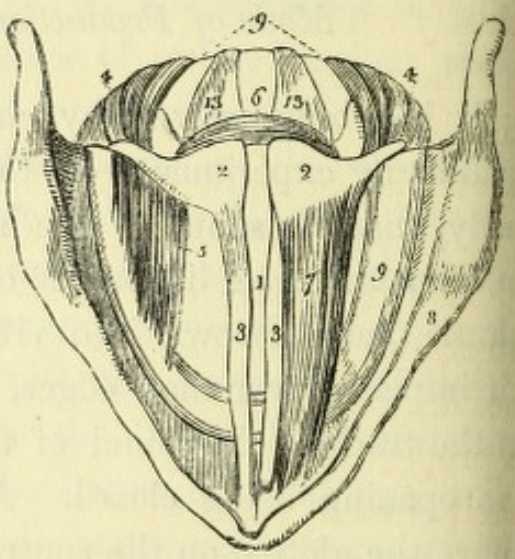



*Fig.* 53.†




* Fig. 52. Lateral view of exterior of larynx, after Mr. Willis (xliii. 1832).—8. Thyroid cartilage. 9. Cricoid cartilage. 10. Crico-thyroid muscle. 11. Crico-thyroid ligament. 12. First rings of trachea.

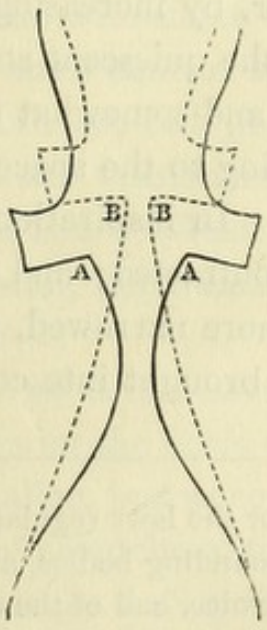
† Fig. 53. View of interior of larynx from above.—1. Aperture of glottis. 2. Arytenoid cartilages. 3. Vocal cords. 4. Posterior crico-arytenoid muscles. 5. Lateral crico-arytenoid muscle of right side, that of left side removed. 6. Arytenoid muscle. 7. Thyro-arytenoid muscle of left side, that of right side removed. 8. Thyroid cartilage. 9. Cricoid cartilage. 13. Posterior crico-arytenoid ligament. With the exception of the arytenoid muscle, this diagram is a copy from Mr. Willis's figure.

are so attached to the cartilaginous parts of the larynx that they can be made tense either by the depression of the thyroid cartilage (figs. 52 and 53,[8]), towards the cricoid cartilage (figs. 52 and 53,[9]) by means of the crico-thyroid muscles (fig. 52,[10]); or by the retraction of the arytenoid cartilages (fig. 53,[2]) which are moved backwards by the posterior crico-arytenoid muscles (fig. 53,[4]), at the same time that they are approximated by the posterior arytenoid ([6]). The length of the fissure of the glottis ([1]) depends on the degree to which the cords are thus stretched; and their degree of tension probably depends not only on the degree in which their stretching is resisted by their proper tissue, but also, in some measure, on the action of the thyro-arytenoid muscles ([7]), which are closely connected to them along their whole length.

The aperture of the glottis is narrowed by the approximation of the arytenoid cartilages, which is effected by the arytenoid muscles: it is dilated by the lateral crico-arytenoid ([5]), which draw the arytenoid cartilages asunder.

The experiments of the Rev. Mr. Willis (cxliii. 1832) on instruments made in imitation of the larynx, have shewn that, besides being made tense, the vocal cords, in order to produce a proper vocal sound, must have their inner edges parallel. In the ordinary position of the glottis, during respiration without vocalization, he supposes that the lips of the glottis are inclined from each other (as at A, fig. 54, which is an imaginary transverse perpendicular section of the vocal tube), and that to produce voice they must assume the parallel state (as at B, fig. 54); and he attributes to the thyro-arytenoid muscles the office of placing the ligaments in this position.

*Fig.* 54.



In vocalizing, the ligaments vibrate in their entire breadth, and with them the thyro-arytenoid muscles, and (to an extent corresponding to the force with which they vibrate) the adjacent elastic tissues of the larynx and other parts, and the air in and beyond the respiratory passages. For the deepest notes, the vocal ligaments are much relaxed by the approximation of the thyroid to the arytenoid cartilages. The lips or margins of the glottis are, in this state of the larynx, not only devoid of tension—they are, when at rest, even wrinkled—but they become stretched by the current of air, and thus acquire the degree of tension necessary for vibration. From the deepest note thus produced, the vocal sounds may be raised about an octave, by allowing the vocal cords to have the slight degree of tension which the elastic crico-thyroid ligament can give them, by drawing the thyroid cartilage towards the cricoid. The medium state, in which the cords are neither relaxed and wrinkled, nor stretched, is the condition for the middle notes of the natural voice, and those which are most easily produced in singing. (The ordinary tones of the voice in speaking are intermediate between these and the deep bass notes.) The higher notes of the natural voice are produced by the lateral compression of the vocal cords, and the narrowing of the space between them by means of the thyro-arytenoid muscles; and further, by increasing the force of the current of air.*

In the quiescent state, the aperture of the glottis is widely open, and somewhat triangular, the base of the triangle corresponding to the space between the separated arytenoid cartilages. In inspiration, the glottis is slightly dilated, in expiration contracted; and at the moment of the emission of sound, it is more narrowed, the margins of the arytenoid cartilages being brought into contact, and the edges of the vocal cords

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* For the laws regulating the vibration of membranous tongues, and other sounding bodies, and for further details of the mode of production of the voice, and of the circumstances by which it is modulated, consult Müller.

approximated and made parallel. The degree of approximation usually corresponds to the height of the note produced; but probably not always, for the width of the aperture has no essential influence on the height of the note, as long as the vocal cords have the same tension; only, with a wide aperture, the tone is more difficult to produce, and is less perfect, the rushing of the air through the aperture being heard at the same time.

No true vocal sound is produced at the posterior part of the aperture of the glottis, that viz., which is formed by the space between the arytenoid cartilages. For, as Müller's experiments showed, if the arytenoid cartilages be approximated in such a manner, that their anterior processes touch each other, but yet leave an opening behind them as well as in front, no second vocal tone is produced by the passage of the air through the posterior opening, but merely a rustling or bubbling sound; and the height or pitch of the note produced is the same whether the posterior part of the glottis be open or not, provided the vocal cords maintain the same degree of tension.

Vocal sounds can be produced not only when the lips of the glottis are separated by a narrow interval, but even when to the eye they appear to be in contact, especially if the vocal cords are much relaxed; in which case the vibrations of the lips of the glottis are very strong. The notes emitted in such a condition of the glottis are stronger and fuller; but, provided the length of the cords be the same, and the tension in both cases equally slight, the height of the note is not influenced by the cords being in contact, or by their being separated by a narrow interval.

The *epiglottis*, by being pressed down so as to cover the superior cavity of the larynx, serves to render the notes deeper in tone, and at the same time somewhat duller, just as covering the end of a short tube placed in front of caoutchouc tongues lowers the tone. In uttering very deep tones during life, we evidently employ the epiglottis in this way; at least such

seems to be the object of the retraction and depression of the tongue while we press down the head in front, in endeavouring to produce very deep notes. In no other respect does the epiglottis appear to have any effect in modifying the vocal sounds.*

### *Application of the Voice in Singing and Speaking.*

The notes of the voice thus produced may observe three different kinds of sequence. The first is the monotonous, in which the notes have nearly all the same pitch as in ordinary speaking; the variety of the sounds of speech being owing to articulation in the mouth. In speaking, however, occasional syllables generally receive a higher intonation for the sake of accent. In poetry there is rhythm in addition to the accent, but the modulation of music is wanting. The second mode of sequence is the successive transition from high to low notes, and *vice versâ*, without intervals; such as is heard in the sounds, which, as expressions of passion, accompany crying in men, and in the howling and whining of dogs. The third mode of sequence of the vocal sounds is the musical, in which each sound has a determinate number of vibrations, and the number of vibrations in the successive sounds have the same relative proportions as characterize the notes of the musical scale.

The *compass of the voice* in different individuals, comprehends one, two, or three octaves. In singers,—that is, in persons apt for singing,—it extends to two or three octaves. But the male and female voices commence and end at different points of the musical scale. The lowest note of the female voice is about an octave higher than the lowest of the male voice; the highest

* The influence which the two portions of the vocal tube, viz., that furnished by the trachea and that by the air-passages in front of the larynx, exercise in modulating the voice, is not yet satisfactorily determined. For observations on the subject, consult Müller (*l. c.*); Mr. Bishop (clxxxi. 1836); and Mr. Willis (cxliii. 1832).

note of the female voice about an octave higher than the highest of the male. The compass of the male and female voices taken together, or the entire scale of the human voice, includes about four octaves. The principal difference between the male and female voice is, therefore, in their pitch; but they are also distinguished by their tone,—the male voice is not so soft.

The voice presents other varieties besides the male and female; there are two kinds of male voice, technically called the bass and tenor, and two kinds of female voice, the contr'alto and soprano, all differing from each other in tone. The bass voice usually reaches lower than the tenor, and its strength lies in the low notes; while the tenor voice extends higher than the bass. The contr'alto voice has generally lower notes than the soprano, and is strongest in the lower notes of the female voice; while the soprano voice reaches higher in the scale. But the difference of compass, and of power in different parts of the scale, is not the essential distinction between the different voices; for bass singers can sometimes go very high, and the contr'alto frequently sings the high notes like soprano singers. The essential difference between the bass and tenor voices, and between the contr'alto and soprano, consists in their tone or "timbre," which distinguishes them even when they are singing the same note. The qualities of the barytone and mezzo-soprano voices are less marked; the barytone being intermediate between the bass and tenor, the mezzo-soprano between the contr'alto and soprano. They have also a middle position as to pitch in the scale of the male and female voices.

The different pitch of the male and the female voice depends on the different length of the vocal cords in the two sexes; their relative length in men and women being as three to two. The difference of the two voices in tone or "timbre," is owing to the different nature and form of the resounding walls, which in the male larynx are much more extensive, and form a more acute angle anteriorly. The different qualities of the tenor and bass, and of the alto and soprano voices, probably depend on

some peculiarities of the ligaments, and the membranous and cartilaginous parietes of the laryngeal cavity, which are not at present understood, but of which we may form some idea, by recollecting that musical instruments made of different materials, *e. g.*, metallic and gut-strings, may be tuned to the same note, but that each will give it with a peculiar tone or "timbre."

The larynx of boys resembles the female larynx; their vocal cords before puberty have not two-thirds the length which they acquire at that period; and the angle of their thyroid cartilage is as little prominent as in the female larynx. Boys' voices are alto and soprano, resembling in pitch those of women, but louder, and differing somewhat from them in tone. But, after the larynx has undergone the change produced during the period of development at puberty, the boy's voice becomes bass or tenor. While the change of form is taking place, the voice is said to "crack;" it becomes imperfect, frequently hoarse and crowing, and is unfitted for singing until the new tones are brought under command by practice. In eunuchs, who have been deprived of the testes before puberty, the voice does not undergo this change. The voice of most old people is deficient in tone, unsteady, and more restricted in extent: the first defect is owing to the ossification of the cartilages of the larynx and the altered condition of the vocal cord; the want of steadiness arises from the loss of nervous power and command over the muscles; the result of which is here, as in other parts, a tremulous motion. These two causes combined render the voices of old people void of tone, unsteady, bleating, and weak.

In any class of persons arranged, as in an orchestra, according to the characters of voices, each would possess, with the general characteristics of a bass, or tenor, or any other kind of voice, some peculiar character by which his voice would be recognised from all the rest. The conditions that determine these distinctions are, however, quite unknown. They are probably inherent in the tissues of the larynx, and are as indis-

cernible as the minute differences that characterise men's features; one often observes, in like manner, hereditary and family peculiarities of voice as well marked as those of the limbs or face.

Most persons, particularly men, have the power, if at all capable of singing, of modulating their voices through a double series of notes of different character: namely, the notes of the natural voice, or *chest-notes*, and the *falsetto notes*. The natural voice, which alone has been hitherto considered, is fuller, and excites a distinct sensation of much stronger vibration and resonance than the falsetto voice, which has more a flute-like character. The deeper notes of the male voice can be produced only with the natural voice, the highest with the falsetto only, the notes of middle pitch can be produced either with the natural or falsetto voice; the two registers of the voice are, therefore, not limited in such a manner as that one ends when the other begins, but they run in part side by side.

The natural, or chest-notes, are produced by the ordinary vibrations of the vocal cords. The mode of production of the falsetto notes is still obscure. By Müller they are thought to be due to vibrations of only the inner borders of the vocal cords. In the opinion of Petrequin and Diday (xix.), they do not result from vibrations of the vocal cords at all, but from vibration of the air passing through the aperture of the glottis, which they believe assumes, at such times, the contour of the *embouchure* of a flute. Others (considering some degree of similarity which exists between the falsetto notes and the peculiar tones, called harmonic, which are produced when, by touching or stopping a harp-string at a particular point, only a portion of its length is allowed to vibrate) have supposed that, in the falsetto notes, portions of the vocal ligaments are thus isolated and made to vibrate while the rest are held still. The question cannot yet be settled: but any one in the habit of singing may assure himself, both by the difficulty of passing smoothly from one set of notes to the other, and by the necessity of exercising himself in both registers lest he should

become very deficient in one, that there must be some great difference in the modes in which their respective notes are produced.

The strength of the voice depends partly on the degree of capability of vibration of the vocal cords; and partly on the fitness for resonance of the membranes and cartilages of the larynx, of the parietes of the thorax, lungs, and cavities of the mouth, nostrils, and communicating sinuses. It is diminished by anything which interferes with such capability of vibration. The intensity or loudness of a given note cannot be rendered greater by merely increasing the force of the current of air through the glottis; for increase of the force of the current of air, *cæteris paribus*, raises the pitch both of the natural and the falsetto notes. Yet, since a singer possesses the power of increasing the loudness of a note from the faintest "piano" to "fortissimo" without its pitch being altered, there must be some means of compensating the tendency of the vocal cords to emit a higher note when the force of the current of air is increased. This means evidently consists in modifying the tension of the vocal cords. When a note is rendered louder and more intense, the vocal cords must be relaxed by remission of the muscular action, in proportion as the force of the current of the breath through the glottis is increased. When a note is rendered fainter, the reverse of this must occur.

The length of the larynx and trachea below the vocal ligaments has, according to Müller, no perceptible influence upon the tone or pitch of the voice;—he thinks that the elongation of the vocal tube in front of the glottis by the descent of the larynx, only facilitates the formation of the deep notes, and the shortening of the tube by the ascent of the larynx that of the high notes. Mr. Bishop states, however, that the trachea is not really lengthened by the ascent of the larynx; he finds that it is raised out of the thorax nearly to the same extent as the larynx is elevated; he therefore concludes, that an absolute shortening of the entire vocal tube, including the trachea, and the cavities above the glottis, is produced by the elevation

of the larynx towards the base of the skull. But the variation in the length of the tube being insufficient to render it capable of adjusting itself to the whole range of vocal tones, both he and Mr. Wheatstone (clxxxii. p. 373) suppose that the defect is supplied by the varying tension of the walls of the trachea, and by the diminished diameter of the trachea during the ascent of the larynx. A still further influence on the voice is attributed to the trachea by Mr. Wheatstone. He has observed that a column of air may not only vibrate, by reciprocation with another body whose vibrations are isochronous with its own, but also when the number of its own vibrations are any multiple of those of the sounding body. Such would be the vibrations of the column of air in the trachea divided into harmonic lengths, with relation to the vibrations of the vocal cords. The falsetto notes, he suggests, may be the result of the vibrations of the harmonic subdivisions of the column of air in the trachea.

The *arches of the palate and the uvula* become contracted during the formation of the higher notes: but their contraction is the same for a note of given height, whether it be falsetto or not: and in either case the arches of the palate may be touched with the finger, without the note being altered. Their action, therefore, in the production of the higher notes, seems to be merely the result of involuntary associate nervous action, excited by the voluntarily increased exertion of the muscles of the larynx. If the palatine arches contribute at all to the production of the higher notes of the natural voice and the falsetto, it can only be by their increased tension strengthening the resonance.

The office of the *ventricles of the larynx* is evidently to afford a free space for the vibrations of the lips of the glottis; they may be compared with the cavity at the commencement of the mouth-piece of trumpets, which allows the free vibration of the lips.*

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* Many of the conclusions respecting the physiology of the human

## SPEECH.

Besides the musical tones formed in the larynx, a great number of other sounds can be produced in the vocal tube, between the glottis and the external apertures of the air-passages, the combination of which sounds into different groups to designate objects, properties, actions, etc., constitutes *language*. The languages do not employ all the sounds which can be produced in this manner, the combination of some with others being often difficult. Those sounds which are easy of combination enter, for the most part, into the formation of the greater number of languages. Each language contains a certain number of such sounds, but in no one are all brought together. On the contrary, different languages are characterised by the prevalence in them of certain classes of these sounds, while others are less frequent or altogether absent.

The sounds produced in speech, or *articulate sounds*, are commonly divided into *vowels* and *consonants;* the distinction between which is, that the sounds for the former are generated by the larynx, while those for the latter are produced by interruption of the current of air in some part of the air-passages above the larynx. The term consonant has been given to these because several of them are not properly sounded, except *consonantly with* a vowel. Thus, if it be attempted to pronounce aloud the consonants *b*, *h*, and *g*, or their modifications *p*, *t*, *k*, the intonation only follows them, in their combination with a vowel.

To recognise the essential properties of the articulate sounds, we must, according to Müller, first examine them as they are

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voice which are stated in the foregoing pages are derived from, or illustrated by, experiments with apparatus made in imitation of the larynx; for the complete account of these, and for suggestions how they may be yet further applied to the study of this part of physiology, consult the elaborate chapters by Müller; and the papers of Willis (cxliii. 1832); Wheatstone (clxxxii.); Bishop (clxxxi. 1836); and the earlier writers to whom Müller refers.

produced in whispering, and then investigate which of them can also be uttered in a modified character conjoined with vocal tone. By this procedure we find two series of sounds: in one the sounds are mute, and cannot be uttered with a vocal tone; the sounds of the other series can be formed independently of voice, but are also capable of being uttered in conjunction with it.

All the vowels can be expressed in a whisper without vocal tone, that is, mutely. These mute vowel-sounds differ, however, in some measure, as to their mode of production, from the consonants. All the mute consonants are formed in the vocal tube above the glottis, or in the cavity of the mouth or nose, by the mere rushing of the air between surfaces differently modified in disposition. But the sound of the vowels, even when mute, has its source in the glottis, though the vocal cords are not thrown into the vibrations necessary for the production of voice; and the sound seems to be produced by the passage of the current of air between the relaxed vocal cords. The same vowel-sound can be produced in the larynx when the mouth is closed, the nostrils being open, and the utterance of all vocal tone avoided. This sound, when the mouth is open, is so modified by varied forms of the oral cavity, as to assume the characters of the vowels *a*, *e*, *i*, *o*, *u*, in all their modifications.

The cavity of the mouth assumes the same form for the articulation of each of the mute vowels as for the corresponding vowel when vocalized; the only difference in the two cases lies in the kind of sound emitted by the larynx. Kratzenstein and Kempelen have pointed out that the conditions necessary for changing one and the same sound into the different vowels, are differences in the size of two parts—the oral canal and the oral opening; and the same is the case with regard to the mute vowels. By oral canal, Kempelen means here the space between the tongue and palate: for the pronunciation of certain vowels both the opening of the mouth and the space just mentioned are wide; for the pronunciation of other vowels

both are contracted; and for others one is wide, the other contracted. Admitting five degrees of size, both of the opening of the mouth and of the space between the tongue and palate, Kempelen thus states the dimensions of these parts for the following vowel sounds:—

| Vowel. | Sound. | Size of oral opening. | Size of oral canal. |
|---|---|---|---|
| *a* | as in 'far' | 5 | 3 |
| *a* | „ 'name' | 4 | 2 |
| *e* | „ 'theme' | 3 | 1 |
| *o* | „ 'go' | 2 | 4 |
| *oo* | „ 'cool' | 1 | 5 |

Another important distinction in articulate sounds is, that the utterance of some is only of momentary duration, taking place during a sudden change in the conformation of the mouth, and being incapable of prolongation by a continued expiration. To this class belong *b*, *p*, *d*, and the hard *g*. In the utterance of other consonants the sounds may be *continuous;* they may be prolonged, *ad libitum*, as long as a particular disposition of the mouth and a constant expiration are maintained. Among these consonants are *h*, *m*, *n*, *f*, *s*, *r*, *l*. Corresponding differences in respect to the time that may be occupied in their utterance exist in the vowel-sounds, and principally constitute the differences of long and short syllables. Thus, the *a* as in "far" and "fate," the *o* as in "go" and "fort," may be indefinitely prolonged; but the same vowels (or more properly different vowels expressed by the same letters), as in "can" and "fact," in "dog" and "rotten," cannot be prolonged.*

All sounds of the first or explosive kind are insusceptible of combination with vocal tone ("intonation"), and are absolutely mute; nearly all the consonants of the second or continuous kind may be attended with "intonation."

* The minuter physiology of speech may be best studied in Müller (xxxii.); or in the remarkable work by Ammann (from which even Müller has been instructed), entitled "Dissertatio de Loquela," 1700.

The peculiarity of speaking, to which the term *ventriloquism* is applied, appears to consist merely in the varied modification of the sounds produced in the larynx, in imitation of the modifications which voice ordinarily suffers from distance, etc. From the observations of Müller and Colombat (xxxviii. 1840) it seems that the essential mechanical parts of the process of ventriloquism consist in taking a full inspiration, then keeping the muscles of the chest and neck fixed, and speaking with the mouth almost closed, and the lips and lower jaw as motionless as possible, while air is very slowly expired through a very narrow glottis; care being taken also, that none of the expired air passes through the nose. But, as observed by Müller, much of the ventriloquist's skill in imitating the voices coming from particular directions, consists in deceiving other senses than hearing. We never distinguish very readily the direction in which sounds reach our ear; and, when our attention is directed to a particular point, our imagination is very apt to refer to that point whatever sounds we may hear.

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## CHAPTER XVIII.

### THE SENSES.

SENSATION consists in the mind receiving, through the medium of the nervous system, and, usually, as the result of the action of an external cause, a knowledge of certain qualities or conditions, not of external bodies but of the nerves of sense themselves; and these qualities of the nerves of sense are in all different, the nerve of each sense having its own peculiar quality.

There are two principal kinds of sensation, named common and special. The first is the consequence of the ordinary sensibility or feeling possessed by most parts of the body, and is manifested when a part is touched, or in any ordinary manner is stimulated. According to the stimulus, the mind perceives a sensation of heat, or cold, of pain, of the contact of hard, soft, smooth, or rough objects, etc. From this, also, in morbid states, the mind perceives, itching, tingling, burning, aching, and the like sensations. In its greatest perfection common sensibility constitutes *touch* or *tact*. Touch is, indeed, usually classed with the special senses, and will be considered in the same group with them; yet it differs from them in being a property common to many nerves, *e.g.*, all the sensitive spinal nerves, the pneumogastric, glosso-pharyngeal, and fifth cerebral nerves, and in its impressions being communicable through many organs.

Including the sense of touch, the special senses are five in number, the senses of smell, sight, hearing, taste, and touch. The manifestation of each of the first three depends on the existence of a special nerve; the optic for the sense of sight, the auditory for that of hearing, and the olfactory for that of smell. The sense of taste appears to be a property common to branches of the fifth and of the glosso-pharyngeal nerves.

The senses, by virtue of the peculiar properties of their several nerves, make us acquainted with the states of our own body; and thus, indirectly inform us of such qualities and changes of external matter as can give rise to changes in the condition of the nerves. That which through the medium of our senses is actually perceived by the mind is, indeed, merely a property or change of condition of our nerves; but the mind is accustomed to interpret these modifications in the state of the nerves produced by external influences as properties of the external bodies themselves. This mode of regarding sensations is so habitual in the case of the senses which are more rarely affected by internal causes, that it is only on reflection that we perceive it to be erroneous. In the case of the sense of

feeling or touch, on the contrary, where the peculiar sensations of the nerves perceived by the sensorium are excited as frequently by internal as by external causes, we more readily apprehend the truth. For it is easily conceived that the feeling of pain or pleasure, for example, is due to a condition of the nerves, and is not a property of the things which excite it. What is true of these is true of all other sensations; the mind perceives conditions of the optic, olfactory, and other nerves specifically different from that of their state of rest; these conditions may be excited by the contact of external objects, but they may also be the consequence of internal changes: in the former case the mind, having knowledge of the object through either instinct or instruction, recognises it by the appropriate changes which it produces in the state of the nerves.

The special susceptibility of the different nerves of sense for certain influences,—as of the optic nerve for light, of the auditory nerves for vibrations, and so on,—is not due entirely to those nerves having each a specific irritability for such influences exclusively. For although, in the ordinary events of life, the optic nerve is excited only by the undulations or emanations of which light may consist, the auditory only by vibrations of the air, and the olfactory only by odorous particles, yet each of these nerves may have its peculiar properties called forth by other conditions. In fact, in whatever way, and to whatever degree a nerve of special sense is stimulated, the sensation produced is essentially of the same kind; irritation of the optic nerve invariably producing a sensation of light, of the auditory nerve a sensation of some modification of sound. The phenomenon must therefore be ascribed to a peculiar quality belonging to each nerve of special sense. It has been supposed, indeed, that irritation of a nerve of special sense when excessive may produce pain; but experiments seem to have proved that none of these nerves possess the faculty of common sensibility. Thus Magendie observed that when the olfactory nerves laid bare in a dog were pricked, no signs of

pain were manifested; and other experiments of his seemed to shew that both the retina and optic nerve are insusceptible of pain (lxii. t. iv. p. 180).

External impressions on a nerve can give rise to no kind of sensation which cannot also be produced by internal causes, exciting changes in the condition of the same nerve. In the case of the sense of touch, this is at once evident. The sensations of the nerves of touch (or common sensibility), excited by causes acting from without, are those of cold and heat, pain and pleasure, and innumerable modifications of these, which have the same kind of sensation as their element. All these sensations are constantly being produced by internal causes, in all parts of our body endowed with sensitive nerves. The sensations of the nerves of touch are therefore states or qualities proper to themselves, and merely rendered manifest by exciting causes, whether external or internal. The sensation of smell, also, may be perceived independently of the application of any odorous substance from without, through the influence of some internal condition of the nerve of smell. The sensations of the sense of vision, namely, colour, light and darkness, are also often perceived independently of all external exciting causes. So, also, whenever the auditory nerve is in a state of excitement, the sensations peculiar to it, as the sounds of ringing, humming, etc., are perceived.

The same cause, whether internal or external, excites in the different senses different sensations; in each sense the sensations peculiar to it. For instance, one uniform *internal* cause, which may act on all the nerves of the senses in the same manner, is the accumulation of blood in their capillary vessels, as in congestion and inflammation. This one cause excites in the retina, while the eyes are closed, the sensation of light and luminous flashes; in the auditory nerve, the sensation of humming and ringing sounds; in the olfactory nerve, the sense of odours; and in the nerves of feeling, the sensation of pain. In the same way, also, a narcotic substance introduced into the blood, excites in the nerves of each sense

peculiar symptoms; in the optic nerves, the appearance of luminous sparks before the eyes; in the auditory nerves, "tinnitus aurium;" and in the common sensitive nerves, the sensation of creeping over the surface. So, also, among *external* causes, the stimulus of electricity, or the mechanical influence of a blow, concussion, or pressure, excites in the eye the sensation of light and colours; in the ear, a sense of a loud sound or of ringing; in the tongue, a saline or acid taste; and at the other parts of the body, a perception of peculiar jarring or of the mechanical impression, or a shock like it.

Although, in the cases just referred to, and in all ordinary conditions, sensations are derived from peculiar conditions of the nerves of sense, whether excited by external or by internal causes, yet the mind may have the same sensations independently of changes in the conditions of at least the peripheral portions of the several nerves, and even independently of any connection with the external organs of the senses. The causes of such sensations are seated in the parts of the brain in which the several nerves of sense terminate. Thus pressure on the brain has been observed to cause the sensation of light; luminous spectra may be excited by internal causes after complete amaurosis of the retina: and Humboldt states, that, in a man who had lost one eye, he produced by means of galvanism, luminous appearances on the blind side. Many of the various morbid sensations attending diseases of the brain, the vision of spectra, and the like, are of the same kind.

Again, although the immediate objects of the perception of our senses are merely particular states induced in the nerves, and felt as sensations, yet, inasmuch as the nerves of the senses are material bodies, and therefore participate in the properties of matter generally, occupying space, being susceptible of vibratory motion, and capable of being variously changed chemically, as well as by the action of heat and electricity, they make known to the mind, by virtue of the different changes thus produced in them by external causes, not

merely their own condition, but also some of the different properties and changes of condition of external bodies; as, *e. g.* "extension," progressive and tremulous motion, chemical change, etc. The information concerning external nature thus obtained by the senses, varies in each sense, having a relation to the peculiar qualities or energies of the nerve.

All the senses are not equally adapted to impart the idea of *extension.* The nerve of vision and the nerves of touch, being capable of an exact perception of this property in themselves, make us acquainted with it in external bodies: and it is by seeing and feeling bodies, that we best learn their extension and their relation to other objects and to ourselves. In the nerves of taste, the sensation of extension is less distinct, but not altogether deficient; for we are capable of distinguishing whether the seat of a bitter or sweet taste be the tongue, the palate, or the fauces. The sense of hearing is almost totally incapable of perceiving the quality of extension; for the organ of hearing has no conception of its own extension, or of the part at which the sound is heard. The mind can perceive, at least, the organ on which odours are impressed, and is conscious of the whole cavity of the nostrils being occupied by a penetrating odour; but we cannot make the odorous substance act on less than the entire nasal cavity.

The *sensation of motion* is, like motion itself, of two kinds,—progressive and vibratory. The faculty of the perception of progressive motion is possessed by the senses of vision, touch, and taste. Thus an impression is perceived travelling from one part of the retina to another, and the movement of the image is interpreted by the mind as the motion of the object. The same is the case in the sense of touch; so also the movement of a sensation of taste over the surface of the organ of taste, can be recognised. The motion of tremors, or vibrations, is perceived by several senses, but especially by those of hearing and touch. For the sense of hearing, vibrations constitute the ordinary stimulus, and so give rise to the perception of sound. By

the sense of touch vibrations are perceived as tremors, occasionally attended with the general impression of tickling; for instance, when a vibrating body, such as a tuning-fork, is approximated to a very sensible part of the surface, the eye can communicate to the mind the image of a vibrating body, and can distinguish the vibrations when they are very slow; but the vibrations are not communicated to the optic as to the auditory nerve in such a manner that it repeats them, or receives their impulses.

We are made acquainted with *chemical actions* principally by taste, smell and touch, and by each of these senses in the mode proper to it. Volatile bodies disturbing the conditions of the nerves by a chemical action, exert the greatest influence upon the organ of smell; and many matters act on that sense which produce no impression upon the organs of taste and touch,—for example, many odorous substances, as the vapours of metals, such as lead, and the vapour of many minerals. Some volatile substances, however, are perceived not only by the sense of smell, but also by the senses of touch and taste, provided they are of a nature adapted to disturb chemically the condition of those organs, and in the case of the organ of taste, to be dissolved by the fluids covering it. Thus, the vapours of horse-radish and mustard, and acrid suffocating gases, act upon the conjunctiva and the mucous membrane of the lungs, exciting through the common sensitive nerves, merely modifications of common feeling; and at the same time they excite the sensations of smell and of taste.

Sensations are referred from their proper seat towards the exterior; but this is owing, not to anything in the nature of the nerves themselves, but to the accompanying idea derived from experience. For in the perception of sensations, there is a combined action both of the mind and of the nerves of sense; and the mind, by education or experience, has learned to refer the impressions it receives to objects external to the body. Even when it derives impressions from internal causes, it commonly refers them to external objects. The light perceived in

congestion of the retina seems external to the body: the ringing of the ears in disease is felt as if the sound came from some distance: the mind referring it to the outer world from which it is in the habit of receiving the like impression (see p. 385.

Moreover, the mind not only perceives the sensations and interprets them according to ideas previously obtained, but it has a direct influence upon them, imparting to them intensity by its faculty of attention. Without simultaneous attention, all sensations are only obscurely, if at all, perceived. If the mind be torpid in indolence, or if the attention be withdrawn from the nerves of sense in intellectual contemplation, deep speculations, or an intense passion, the sensations of the nerves make no impression upon the mind; they are not perceived,—that is to say, they are not communicated to the conscious "self," or with so little intensity, that the mind is unable to retain the impression, or only recollects it some time after, when it is freed from the preponderating influence of the idea which had occupied it.

This power of attention to the sensations derived from a single organ, may also be exercised in a single portion of a sentient organ, and thus enable one to discern the detail of what would otherwise be a single sensation. For example, by well-directed attention, one can distinguish each of the many tones simultaneously emitted by an orchestra, and can even follow the weaker tones of one instrument apart from the other sounds, of which the impressions being not attended to are less vividly perceived. So, also, if one endeavours to direct attention to the whole field of vision at the same time nothing is seen distinctly; but when the attention is directed first to this, then to that part, and analyses the detail of the sensation, the part to which the mind is directed is perceived with more distinctness than the rest of the same sensation.

## THE SENSE OF SMELL.

The sense of smell ordinarily requires, for its excitement to a state of activity, the action of external matters, which action produces certain changes in the olfactory nerve; and this nerve is susceptible of an infinite variety of states dependant on the nature of the external stimulus.

The first condition essential to the sense of smell is the existence of a special nerve, the changes in whose condition are perceived as sensations of odour; for no other nerve is capable of these sensations, even though acted on by the same causes. The same substance which excites the sensation of smell in the olfactory nerves, may cause another peculiar sensation through the nerves of taste, and may produce an irritating and burning sensation on the nerves of touch; but the sensation of odour is yet separate and distinct from these, though it may be simultaneously perceived. The second condition of smell is a peculiar state of the olfactory nerve, or a peculiar change produced in it by the stimulus or odorous substance.

The material causes of odours are, in the case of animals living in the air, substances suspended in a state of extremely fine division in the atmosphere; or gaseous exhalations, often of so subtile a nature that they can be detected by no other reagent than the sense of smell itself. In fishes, the odorous matters are contained in the water; but in what form,—whether dissolved in the same manner as the gases absorbed by water—is uncertain. The matters of odour must, in all cases, be dissolved in the mucus of the mucous membrane before they can be immediately applied to, or affect, the olfactory nerves; therefore a further condition necessary for the perception of odours is, that the mucous membrane of the nasal cavity be moist. When the Schneiderian membrane is dry, the sense of smell is lost; in the first stage of catarrh, when the secretion of mucus within the nostrils is lessened,

the faculty of perceiving odours is either lost, or rendered very imperfect.

In animals living in the air, it is also requisite that the odorous matters should be transmitted in a current through the nostrils. This is effected by the respiratory movements: hence we have voluntary influence over the sense of smell; for by interrupting respiration we prevent the perception of odours, and by repeated quick inspirations assisted, as in the act of *sniffing*, by slight contraction of the nostrils, we render the impression more intense.

The human organ of smell is essentially formed by the filaments of the olfactory nerves distributed in minute arrangement, in the mucous membrane covering the superior three-fourths of the septum of the nose, the superior turbinated or spongy bone, the upper half of the middle turbinated bone, and the upper wall of the nasal cavities beneath the cribriform plates of the ethmoid bone. This olfactory region is covered by tesselated epithelium (Todd and Bowman). In all their distribution, the branches of the olfactory nerves retain much of the same soft and greyish texture which distinguishes their trunks (as the olfactory lobes of the brain are called) within the cranium. Their individual filaments, also, are peculiar, more resembling those of the sympathetic nerve than the filaments of the other cerebral nerves do, containing no outer white substance, and being finely granular and nucleated.* The branches are distributed principally in close plexuses; but the mode of termination of the filaments is not yet satisfactorily determined.

The sense of smell is derived exclusively through those parts of the nasal cavities in which the olfactory nerves are distributed; the accessory cavities or sinuses communicating with

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* See Todd and Bowman (xxxix. vol. ii.): the work which, before all, on the minute anatomy of the organs of sense, the student should consult.

the nostrils seem to have no relation to it. Air impregnated with the vapour of camphor was injected by Deschamps into the frontal sinus through a fistulous opening, and Richerand injected odorous substances into the antrum of Highmore; but in neither case was any odour perceived by the patient. The purposes of these sinuses appear to be, that the bones, necessarily large for the action of the muscles and other parts connected with them, may be as light as possible, and that there may be more room for the resonance of the air in vocalizing. The former purpose, which is in other bones obtained by filling their cavities with fat, is here attained, as it is in many bones of birds, by their being filled with air.

All parts of the nasal cavities, whether or not they can be the seats of the sense of smell, are endowed with common sensibility by the nasal branches of the first and second divisions of the fifth nerve. Hence the sensations of cold, heat, itching, tickling, and pain; and the sensation of tension or pressure in the nostrils. That these nerves cannot perform the function of the olfactory nerves is proved by cases in which the sense of smell is lost, while the mucous membrane of the nose remains susceptible of the various modifications of common sensation or touch. But it is often difficult to distinguish the sensation of smell from that of mere feeling, and to ascertain what belongs to each separately. This is the case particularly with the sensations excited in the nose by acrid vapours, as of ammonia, horse-radish, mustard, etc., which resemble much the sensations of the nerves of touch; and the difficulty is the greater, when it is remembered that these acrid vapours have nearly the same action upon the mucous membrane of the eyelids. It was because the common sensibility of the nose to these irritating substances remained, after the destruction of the olfactory nerves, that Magendie was led to believe the fifth nerve might exercise the special sense.

Animals do not all equally perceive the same odours; the odours perceived by an herbivorous animal and by a carnivorous animal are different. The Carnivora have the power of

detecting most accurately by the smell the special peculiarities of animal matters, and of tracking other animals by the scent; but have apparently no sensibility to the odours of plants and flowers. Herbivorous animals are peculiarly sensitive to the latter, and have a narrower sensibility to animal odours, especially to such as proceed from other individuals than their own species. Man is far inferior to many animals of both classes in respect of the acuteness of smell: but his sphere of susceptibility to various odours is more uniform and extended. The cause of this difference must lie in the endowments of the central parts of the olfactory apparatus.

Opposed to the sensation of an agreeable odour is that of a disagreeable or disgusting odour, which corresponds to the sensations of pain, dazzling and disharmony of colours, and dissonance, in the other senses. The cause of this difference in the effect of different colours is unknown; but this much is certain, that odours are pleasant or offensive in a relative sense only, for many animals pass their existence in the midst of odours which to us are highly disagreeable. A great difference in this respect is, indeed, observed amongst men: many odours generally thought agreeable are to some persons intolerable; and different persons describe differently the sensations that they severally derive from the same odorous substances. There seems also to be in some persons an insensibility to certain odours, comparable with that of the eye to certain colours; and among different persons, as great a difference in the acuteness of the sense of smell as among others in the acuteness of sight. We have no exact proof that a relation of harmony and disharmony exists between odours as between colours and sounds; though it is probable that such is the case, since it certainly is so with regard to the sense of taste; and since such a relation would account in some measure for the different degrees of perceptive power in different persons; for as some have no ear for music (as it is said), so others have no clear appreciation of the relation of odours, and, therefore, little pleasure in them. It is also not certain that sensations of

odours continue after the impression of the odorous matter has ceased, though we can scarcely imagine that such is not the case. It is difficult to ascertain this point by direct observation; because the odour that is frequently retained in the nose may arise from some of the odorous matter remaining dissolved in the mucus of the nostrils.

The sensations of the olfactory nerves, independent of the external application of odorous substances, have hitherto been little studied. It has been found that solutions of inodorous substances, such as salts, excite no sensation of odour when injected into the nostrils. The friction of the electric machine is, however, known to produce a smell like that of phosphorus. Ritter, too, has observed, that when galvanism is applied to the organ of smell, besides the impulse to sneeze, and the tickling sensation excited in the filaments of the fifth nerve, a smell like that of ammonia was excited by the negative pole, and an acid odour by the positive pole; whichever of these sensations was produced, it remained constant as long as the circle was closed, and changed to the other at the moment of the circle being opened. Frequently a person smells something which is not present, and which other persons cannot smell; this is very frequent with nervous people, but it occasionally happens to every one. In a man who was constantly conscious of a bad odour, the arachnoid was found after death, by MM. Cullerier and Maignault, to be beset with deposits of bone; and in the middle of the cerebral hemispheres were scrofulous cysts in a state of suppuration. Dubois was acquainted with a man who, ever after a fall from his horse, which occurred several years before his death, believed that he smelt a bad odour.

## THE SENSE OF SIGHT.

The eye, or the organ of vision, consists essentially in a membranous expansion of the peripheral extremity of the nerve of sight, the optic, for the purpose of receiving the impressions of the rays of light from luminous bodies. This expansion of

the optic nerve is termed the *retina*. It is a delicate membrane, concave, with the concavity directed forwards; semi-transparent when fresh, but soon becoming clouded and opaque, with a pinkish tint from the blood in its minute vessels. It results from the sudden spreading out or expansion of the optic nerve, of whose terminal fibres, apparently deprived of their external white substance, it is almost entirely composed. At first the fibres of the optic nerve run in distinct bundles, which radiate from the point at which the trunk of the nerve terminates, and then pursue a tolerably straight course towards the anterior margin of the retina. As they proceed in this course, however, the bundles shortly break up into their component fibres, which then interlace and form a fine membranous sheath, towards the anterior margin of which all trace of fibrous arrangement disappears.

The mode in which the nerve-fibres of the retina terminate, is still involved in obscurity, in spite of the many efforts to determine the question. According to some observers, the fibres terminate in loops, according to others, in free extremities, and according to others, again, they become continuous with prolongations from nerve-cells, which are found abundantly in the tissue of the retina. That the latter is not an unfrequent mode of termination seems to have been fully proved by Kölliker, H. Müller, and others (cxc. vol. xiii. p. 547).

Nearly all who have recently examined the minute structure of the retina, concur in describing the existence of numerous cells and globules lying on both sides of the fibrous expansion of this membrane, and chiefly along its internal surface and within the meshes formed by the interlacing of the individual nerve-fibres. These cellular bodies appear to be of different kinds, although, as Henle observes, it is probable that the several varieties met with, are only the same cells in different stages of development. The larger and more perfectly developed cells are nearest to the fibrous layer. By Valentin (xxxiv. 1837, p. 25), who first accurately described them, they were considered as identical with the ganglion-corpuscles of

nervous substance: and the fact that many of them present radiating processes or prolongations, which, as just stated, not unfrequently become directly continuous with the nerve-fibres of the retina, substantiates this opinion. Very shortly after death, these cells and the place which they occupied become a confused granular mass, in which are scattered, often in a linear direction, numerous oil-like globules, which are probably the nuclei of the disintegrated cells.

Exactly in the centre of the retina, and at a point thus corresponding to the axis of the eye, in which the sense of vision is most perfect, is a round yellowish elevated spot, about $\frac{1}{24}$th of an inch in diameter, having a minute aperture at its summit, and called after its discoverer the *yellow spot of Soemmering*. It is not covered by the fibrous part of the retina, but a layer of closely-set cells passes over it (xxxix. vol. ii. p. 31). The use of this spot is quite unknown. At about an eighth of an inch to the inner side of the yellow spot, and consequently of the axis of the eye, is the point at which the optic nerve spreads out its fibres to form the retina. This is the only point of the surface of the retina from which the power of vision is absent.

On the outside, the retina is surrounded by the *membrana Jacobi*, composed of cylindrical or staff-shaped, transparent, and highly refractive bodies, arranged perpendicularly to the surface of the retina, with their outer extremities imbedded, to a greater or less depth, in a layer of black pigment of the choroid coat. Recent researches seem to have determined that this membrane, instead of being, as was formerly considered, an independent covering, is intimately associated, both in structure and function, with the sensitive part of the retina; for the conical and staff-shaped bodies, of which it is composed, appear to be connected, by means of delicate fibres issuing from them, with the nerve-vesicles of the retina, and even to become continuous with the radiating processes which some of these vesicles present (ccvii. p. 706). Concerning the use of these bodies, Brücke was of opinion that they may serve to

conduct back to the sensitive portion of the retina, those rays of light which, having traversed that membrane, are not entirely absorbed by the black pigment of the choroid; but the discovery of their connection with the sensitive part of the retina supports the opinion entertained by Kölliker and H. Müller, that their special office is to receive and transmit impressions of light.

The choroid which is the next tunic of the eye, and surrounds the membrana Jacobi, consists of a thin and highly vascular membrane, of which the internal surface is covered by a layer of black pigment-cells, in which, as just said, the staff-shaped bodies of the membrana Jacobi are imbedded. The principal use of the choroid is to absorb, by means of its pigment, those rays of light which pass through the transparent retina, and thus to prevent their being thrown again upon the retina, so as to interfere with the distinctness of the images there formed. Hence animals in which the choroid is destitute of pigment, and human Albinoes, are dazzled by daylight, and see best in the twilight.

By means of the retina and the other parts just described, a provision is afforded for enabling the terminal fibres of the optic nerve to receive the impression of rays of light, and to communicate them to the brain, in which they excite the sensation of vision. But that light should produce in the retina images of the objects from which it comes, it is necessary that when emitted or reflected from determinate parts of external objects, it should stimulate only corresponding parts of the retina. For as light radiates from a luminous body in all directions, when the media offer no impediment to its transmission, a luminous point will necessarily illuminate all parts of a surface, such as the retina, opposed to it, and not merely one single point. A retina, therefore, without any optical apparatus placed in front of it to separate the light of different objects, would see nothing distinctly, but would merely perceive the general impression of daylight, and distinguish it from the night. Accordingly, we find that in man, and most

vertebrate animals, certain transparent refracting media are placed in front of the retina for the purpose of collecting together into one point, the different diverging rays emitted by each point of the external body, and of giving them such directions that they shall fall on corresponding points of the retina, and thus produce an exact image of the object from which they proceed. These refracting media are, in the order of succession from without inwards, the cornea, the aqueous humour, the crystalline lens, and the vitreous humour.

The *cornea* is a dense perfectly transparent substance, convex anteriorly, concave posteriorly, and composed of fibrous tissues arranged in numerous distinct laminæ. It is in a twofold manner capable of refracting and causing convergence of the rays of light that fall upon and traverse it. It thus affects them first, by its density; for it is a law in optics that when rays of light pass from a rarer into a denser medium, if they impinge upon the surface in a direction removed from the perpendicular, they are bent out of their former direction towards that of a line perpendicular to the surface of the denser medium; and, secondly, by its convexity—for it is another law in optics that rays of light impinging upon a convex transparent surface, are refracted towards the centre, those being most refracted which are farthest from the centre of the convex surface.

Behind the cornea is a space containing a thin watery fluid, the *aqueous humour*, holding in solution a small quantity of chloride of sodium and extractive matter. The space containing the aqueous humour is divided into an anterior and posterior *chamber* by a membranous partition, *the iris*, to be presently again mentioned. The effect produced by the aqueous humour on the rays of light traversing it, is not yet fully ascertained. Its chief use, probably, is to enable the cornea to maintain its proper convexity, and at the same time to furnish a medium in which the movements of the iris can take place.

Behind the aqueous humour and the iris, and imbedded in

the anterior part of the medium next to be described, viz., the vitreous humour, is seated a doubly-convex body, the *crystalline lens*, which is the most important refracting structure of the eye. The structure of the lens is very complex. It consists essentially of fibres united side by side to each other, and arranged together in very numerous laminæ, which are so placed upon one another, that when hardened in spirit the lens splits into three portions, in the form of sectors, each of which is composed of superimposed concentric laminæ. The lens increases in density and, consequently, in power of refraction, from without inwards; the central part, usually termed the nucleus, being the most dense. The density of the lens increases with age; it is comparatively soft in infancy, but very firm in advanced life: it is also more spherical at an early period of life than in old age.

The *vitreous humour* constitutes nearly four-fifths of the whole globe of the eye. It fills up the space between the retina and the lens, and its soft jelly-like substance consists essentially of nnmerous layers, formed of delicate, simple membrane, the spaces between which are filled with a watery, pellucid fluid. It probably exercises some share in refracting the rays of light to the retina; but its principal use appears to be that of giving the proper distension to the globe of the eye, and of keeping the surface of the retina at a proper distance from the lens.

Such are the transparent media by which the rays of light undergo the necessary refraction in their course from an external object to the sensitive retina. They and the other contents of the ball of the eye are surrounded and kept in position by a dense, fibrous, external investment, termed the *sclerotica*, which, besides thus encasing the contents of the eye, serves to give attachment to the various muscles by which the movements of the eye-ball are effected. These muscles, and the nerves supplying them, have been already considered (p. 447).

As already observed, the space occupied by the aqueous

humour is divided into two portions by a vertically-placed membranous diaphragm, termed the *iris*, provided with a central aperture, the *pupil*, for the transmission of light. The iris is composed of organic muscular fibres imbedded in ordinary fibro-cellular or connective tissue. The muscular fibres of the iris have a direction, for the most part, radiating from the circumference towards the pupil; but as they approach the pupillary margin, they assume a circular direction, and at the very edge form a complete ring. By the contraction of the radiating fibres, the size of the pupil is enlarged: by the contraction of the circular ones, which resemble a kind of sphincter, it is diminished. The object effected by the movements of the iris, is the regulation of the quantity of light transmitted to the retina; the quantity of which is *cæteris paribus*, directly proportioned to the size of the pupillary aperture. The posterior surface of the iris is coated with a layer of dark pigment, so that no rays of light can pass to the retina, except such as are admitted through the aperture of the pupil.*

## *Of the Phenomena of Vision.*

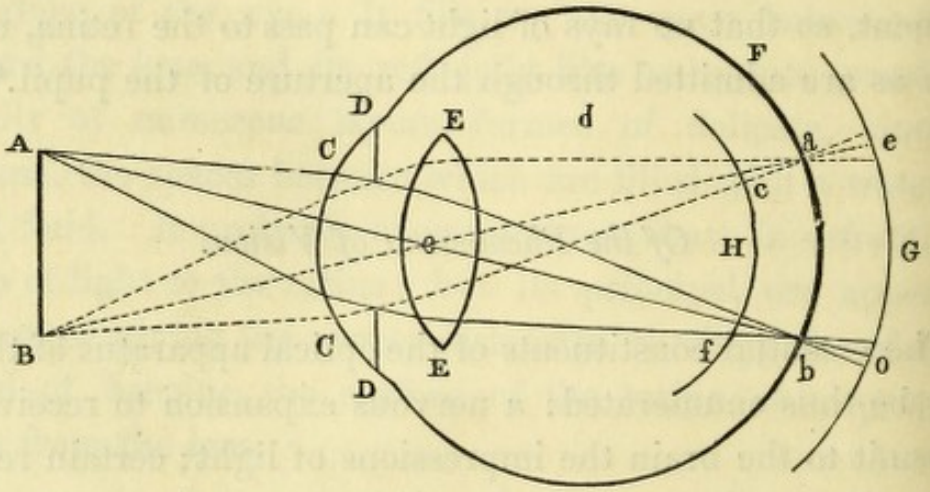
The essential constituents of the optical apparatus of the eye may be thus enumerated: a nervous expansion to receive and transmit to the brain the impressions of light; certain refracting media for the purpose of so disposing of the rays of light traversing them, as to throw a correct image of an external body on the retina; and a contractile diaphragm with a central aperture for regulating the quantity of light admitted into the eye.

With the help of the diagram on the next page (fig. 55),

* For the best account of the structure of the various parts of the eye, see, besides Todd and Bowman (xxxix. vol. ii.), the Lectures on Ophthalmic Surgery, by Mr. Bowman (lxxi. 1847 and 1848); Arnold (clxv.); Lawrence (clxxxv.); Wharton Jones (clxix. and lxxiii. art. *Eye*); Brücke (clxx.); Kölliker (ccvi. and ccxii.), and Nunneley (ccxxx.).

representing a vertical section of the eye from before backwards, the mode in which, by means of the refracting media of the eye, an image of an object of sight is thrown on the retina, may be rendered intelligible. The rays of the cones of light emitted by the points A B, and every other point of an object placed before the eye, are first refracted, that is, are bent towards the axis of the cone, by the cornea C C, and the aqueous humour contained between it and the lens. The rays of each cone are again refracted and bent still more towards its central ray or axis by the anterior surface of the lens E E; and again as they pass out through its posterior surface into the less dense medium of the vitreous humour. For a lens has the power of refracting and causing the convergence of, the rays of a cone of light, not

*Fig.* 55.




only on their entrance from a rarer medium into its anterior convex surface, but also at their exit from its posterior convex surface into the rarer medium.

In this manner the rays of the cones of light issuing from the points A and B are again collected to points at *a* and *b*; and, if the retina F be situated at *a* and *b*, perfect, though reversed, images of the points A and B will be perceived: but if the retina be not at *a* and *b*, but either before or behind that situation,—for instance, at H or G,—circular luminous spots *c* and

*f*, or *e* and *o*, instead of points, will be seen; for at H the rays have not yet met, and at G they have already intersected each other, and are again diverging. The retina must therefore be situated at the proper focal distance from the lens, otherwise a defined image will not be formed; or, in other words, the rays emitted by a given point of the object will not be collected into a corresponding point of focus upon the retina.

The means by which *distinct* and *correct* images of objects are formed in the retina, in the various conditions in which the eye is placed in relation to external objects, may be separately considered under the following heads:—1, the means for preventing indistinctness from aberration; 2, the means for preventing it when objects are viewed at different distances; 3, the means by which the *reversed image* of an object on the retina is perceived as in its right position by the mind.

1. Since the retina is concave, and from its centre towards its margins gradually approaches the lens, it follows that the images of objects situated at the sides cannot be so distinct as those of objects nearer to the middle of the field of vision, and of which the images are formed at a distance behind the lens exactly corresponding to the situation of the retina. Moreover, the rays of a cone of light from an object situated at the side of the field of vision do not meet all in the same point, owing to their unequal refraction; for the refraction of the rays which pass through the circumference of a lens is greater than that of those traversing its central portion. The concurrence of these two circumstances would cause indistinctness of vision, unless corrected by some contrivance. Such correction is effected, in both cases, by the iris, which forms a kind of annular diaphragm to cover the circumference of the lens, and to prevent the rays from passing through any part of the lens but its centre, which corresponds to the pupil.

The image of an object will be most defined and distinct when the pupil is narrow, the object at the proper distance for vision, and the light abundant; so that, while a sufficient number of rays are admitted, the narrowness of the pupil may

prevent the production of indistinctness of the image by this *spherical aberration* or unequal refraction just mentioned. But even the image formed by the rays passing through the circumference of the lens, when the pupil is much dilated, as in the dark, or in a feeble light, may, under certain circumstances, be well defined; the image formed by the central rays being then indistinct or invisible, in consequence of the retina not receiving these rays where they are concentrated to a focus.

Distinctness of vision is further secured by the inner surface of the choroid, immediately external to the retina itself, as well as the posterior surface of the iris and the ciliary processes, being coated with black pigment, which absorbs any rays of light that may be reflected within the eye, and prevents their being thrown again upon the retina so as to interfere with the images there formed. The pigment of the choroid is especially important in this respect; for the retina is very transparent, and if the surface behind it were not of a dark colour, but capable of reflecting the light, the luminous rays which had already acted on the retina would be reflected back again through it, and would fall upon other parts of the same membrane, producing both dazzling from excessive light, and indistinctness of the images.

In the passage of light through an ordinary convex lens, decomposition of each ray into its elementary coloured parts commonly ensues, and a coloured margin appears around the image, owing to the unequal refraction which the elementary colours undergo. In the optical instruments this, which is termed *chromatic aberration*, is corrected by the use of two or more lenses, differing in shape and density, the second of which continues or increases the refraction of the rays produced by the first, but by recombining the individual parts of each ray into its original white light, corrects any chromatic aberration which may have resulted from the first. It is probable that the unequal refractive power of the transparent media in front of the retina, may be the means by which the eye is enabled

to guard against the effect of chromatic aberration. The human eye is achromatic, however, only so long as the image is received at its focal distance upon the retina, or so long as the eye adapts itself to the different distances of sight. If either of these conditions be interfered with, a more or less distinct appearance of colours is produced.

2. The distinctness of the image formed upon the retina is mainly dependent on the rays emitted by each luminous point of the object being brought to a perfect focus upon the retina. If this focus occurs at a point either in front of, or behind the retina, indistinctness of vision ensues, with the production of a halo. The focal distance, *i. e.*, the distance of the point at which the luminous rays from a lens are collected, besides being regulated by the degree of convexity and density of the lens, varies with the distance of the object from the lens, being greater as this is shorter, and *vice versâ*. Hence, since objects placed at various distances from the eye can, within a certain range, different in different persons,* be seen with almost equal distinctness, there must be some provision by which the eye is enabled to adapt itself; so that whatever length the focal distance may be, the focal point may always fall exactly upon the retina.

This power of *adaptation of the eye to vision at different distances* has received the most varied explanations. It is obvious that the effect might be produced in either of two ways; viz., by altering the convexity or density, and thus the refracting power, either of the cornea or lens; or, by changing the position either of the retina or of the lens, so that whether the object viewed be near or distant, and the focal distance thus increased or diminished, the focal point to which the rays are converged by the lens may always be at the place occupied by the retina. The amount of either of these changes required

* An ingenious instrumeut for measuring the distances at which each person may have a distinct sight of objects has been invented by Mr. Smee, who names it the Optometer (clxxxvi.).

in even the widest range of vision, is extremely small. For, from the refractive powers of the media of the eye it has been calculated by Olbers, that the difference between the focal distances of the images of an object at such a distance that the rays are parallel, and of one at the distance of four inches, is only about 0·143 of an inch. On this calculation, the change in the distance of the retina from the lens required for vision at all distances, supposing the cornea and lens to maintain the same form, would not be more than about one line, which might be effected either by elongation of the eye, or by a change in the position of the lens. Dr. Young estimated the necessary change at one sixth of the length of the axis of the eye. Olbers also calculated the amount of change in the convexity of the cornea which would be required for distinct vision at different distances, and finds it to be extremely small, though greater than it appeared probable could be produced by any power of the eye or of its muscles.

Both the above conditions, as well as several others, have been supposed sufficient alone to account for the power of adaptation of the eye. Thus, by Sir E. Home and others, this power has been attributed exclusively to a change in the convexity of the cornea, produced by the muscles of the eye-ball. But the calculations of Olbers shewed that the necessary change was greater than could be produced by the muscles of the eye; and Hueck has recently adduced evidence to prove that no alteration at all in the convexity of the cornea ensues when the eye looks first at a distant and then at a near body. By others the power of adaptation has been ascribed to alterations in the form of the whole globe of the eye, by the action of the muscles. But the action of the straight muscles is merely to retract the eye, and, if resistance were afforded by the cushion of fat behind it, to flatten rather than elongate it; their action might therefore have the effect of adapting the eye to the vision of distant objects: but it is in looking at very near objects, on the contrary, that we are conscious of an effort within the orbit. Moreover, as observed by Volkmann, we do not seem

to possess sufficient power over the recti muscles to produce the combined action of all the four at one time; and except by such combined action, either of all four, or at least of two opposite ones, retraction of the eye-ball could not be effected. Injury of the third pair of nerves, also, whereby paralysis of three of the recti muscles is produced, is not followed by any material disturbance of the power of adaptation; and evidence has been furnished by Hueck to shew that neither the oblique nor straight muscles can in any way exercise sufficient pressure on the eye to affect appreciable alteration in its form, or in the distinctness of an image formed on the retina.

The movements of the iris have been considered the means of adaptation by some physiologists, chiefly from the fact that when distant objects are viewed, the pupil becomes dilated; when near objects, contracted. In general, such movements in the iris might be regarded as merely associate movements, the pupil contracting when the eye is turned inwards, as in the act of looking at a near object, and dilating when the eyes are turned outwards. But contraction of the pupil may ensue when by a voluntary effort, without any change in the position of the axes of the eyes, a near object is regarded; and dilatation of the pupil when a distant object is regarded. The iris may therefore co-operate for the production of distinct vision at different distances; but sufficient evidence that it is not the chief organ for the adaptation, is furnished by the fact, that individuals in whom the iris is wholly wanting may have perfect vision for near, as well as for distant objects. Hueck, also, states, that without altering the direction of the axes of his eyes, or the quantity of light admitted, but merely by fixing his attention on a side object, he was able to widen his pupils as much as one-half more than their former diameter, without there ensuing any indistinctness of the object towards which the eyes were directed.

The opinion now most commonly entertained of the adapting power of the eye, is, that it is mainly due to some alteration either in position or form, or in both, undergone by the

crystalline lens. The arguments stated by Hueck in favour of this view, are, first, that if the eye is watched attentively from the side, the iris will be observed to be bent forwards in the middle, and approximated closer to the cornea, when a near object is viewed, and to become flattened again when the sight is fixed upon a distant object: secondly, that when the fresh eye of a dog is removed and placed before a window, so that through an opening in the sclerotica, a distinct image of the window frame, and an indistinct one of a smaller object, such as a key, held nearer to the eye, are perceived, the latter may be rendered distinct, and the former indistinct, by drawing the lens forward with a needle, inserted through the margin of the cornea.

With respect to the mode in which such an approximation of the lens towards the cornea during the vision of near objects may be affected, different explanations are offered. By some it is supposed to be produced by vascular turgescence of the ciliary processes; the recedence of the lens ensuing on the cessation of the turgescence. By others, and with greater probability, it is supposed to be effected by the contraction of muscular tissue situated in the neighbourhood of the ciliary body and processes.*

This view is supported by the fact that the adapting power of the eye can by many persons be exerted, and often rapidly, by a voluntary effort, quite independent of any alteration in the direction of the axes of the eyes; for it is inconceivable how such an effect can be produced, except by muscular fibres.

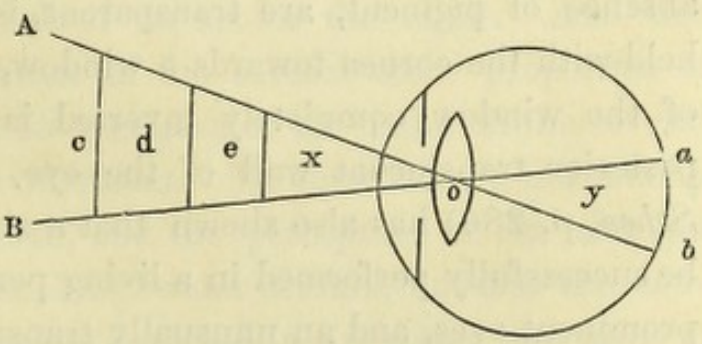
The observations of Volkmann and Hueck, and others, are also favourable to this view; since they shew that in its quiescent state the eye is adapted to the vision of objects situated at the furthest point of distinct sight, and that, therefore, in order to accommodate itself to the vision of an object

* For an analysis of the various opinions on this subject consult the Supplement to Müller's Physiology.

placed at any distance within this far point, the eye will require but one act, that, namely, of increasing its focal distance in proportion to the nearness of the object under view: an act of which the mind seems conscious by the effort which it has to make in adapting the eye to the vision of near objects. No act is requisite to adapt the eye to the perception of distant objects, for, in reverting to its state of rest, it at once resumes its capacity for distant vision, and retains it so long as its quiescent state continues.

The range of distances through which persons can adapt their power of vision is not in all cases the same. Some persons possess scarcely any power of adaptation, and of this defect of vision there are two kinds: one, in which the person can see objects distinctly only when brought close to the eye, having little power to discern distant objects: another, in which distant objects alone can be distinctly perceived, a small body being almost invisible except when held at a considerable distance from the eye. In the one case the person is said to be short-sighted or myopic: in the other, long-sighted or presbyopic. Myopia is caused by anything, such as undue convexity of the cornea, which increases the refracting power of the eye, and so causes the image of the object to be formed at a point anterior to the retina: the defect is remedied by the use of concave glasses. Presbyopia or long-sightedness is the result of conditions the reverse of the above, and is remedied by the use of convex glasses, which diminish the focal distance of an image formed in the eye.*

*Fig.* 56.




* For details on this subject consult Müller (xxxii.) and the various treatises on the Physiology and Defects of Vision.

3. The direction given to the rays by their refraction is regulated by that of the central ray, or axis of the cone, towards which the rays are bent. The image of any point of an object is, therefore, as a rule (the exceptions to which need not here be stated), always formed in a line identical with the axis of the cone of light, as in the line B *a*, or A *b*, fig. 56: so that the spot where the image of any point will be formed upon the retina may be determined by prolonging the central ray of the cone of light, or that ray which traverses the centre of the pupil. Thus, A *b* is the axis or central ray of the cone of light issuing from A; B *a*, the central ray of the cone of light issuing from B; the image of A is formed at *b*, the image of B at *a*, in the inverted position; therefore what in the object was above, is in the image below, and *vice versâ*,—the right-hand part of the object is in the image to the left, the left-hand to the right. If an opening be made in an eye at its superior surface, so that the retina can be seen through the vitreous humours, this reversed image of any bright object, such as the windows of the room, may be perceived at the bottom of the eye. Or still better, if the eye of any albino animal, such as a white rabbit, in which the coats, from the absence of pigment, are transparent, is dissected clean, and held with the cornea towards a window, a very distinct image of the window completely inverted is seen depicted on the posterior translucent wall of the eye, Volkmann (xv. art. *Sehen*, p. 286) has also shewn that a similar experiment may be successfully performed in a living person possessed of large, prominent eyes, and an unusually transparent sclerotica.

No completely satisfactory explanation has yet been offered, to account for the mind being able to form a correct idea of the erect position of an object of which an inverted image is formed on the retina. Müller and Volkmann are of opinion that the mind really perceives an object as inverted but needs no correction, since everything is seen alike inverted, and the relative position of the objects therefore remains unchanged; and the only proof we can possibly have of the inversion is by

experiment and the study of the laws of optics. It is the same thing as the daily inversion of objects consequent on the revolution of the entire earth, which we know only by observing the position of the stars; and yet it is certain that, within twenty-four hours, that which was below in relation to the stars, comes to be above. Hence it is, also, that no discordance arises between the sensations of inverted vision and those of touch, which perceives everything in its erect position; for the images of all objects, even of our own limbs, in the retina, are equally inverted, and therefore maintain the same relative position. Even the image of our hand, while used in touch, is seen inverted. The position in which we see objects, we call therefore the erect position. A mere lateral inversion of our body in a mirror, where the right hand occupies the left of the image, is indeed scarcely remarked: and there is but little discordance between the sensations acquired by touch in regulating our movements by the image in the mirror, and those of sight, as, for example, in tying a knot in the cravat. There is some want of harmony here, on account of the inversion being only lateral, and not complete in all directions.

The perception of the erect position of objects appears, therefore, to be the result of an act of the mind. And this leads us to a consideration of the several other properties of the retina, and of the co-operation of the mind in the several other parts of the act of vision. To these belong not merely the act of sensation itself, and the perception of the changes produced in the retina, as light and colours, but also the conversion of the mere images depicted in the retina into ideas of an extended field of vision, of proximity and distance, of the form and size of objects, of the reciprocal influence of different parts of the retina upon each other, the simultaneous action of the two eyes, and some other phenomena.

To speak first of the *ideal size of the field of vision.*—The actual size of the field of vision depends on the extent of the retina, for only so many images can be seen at any one time as can occupy the retina at the same time; and thus considered,

the retina, of which the affections are perceived by the mind, is itself the field of vision. But to the mind of the individual the size of the field of vision has no determinate limits; sometimes it appears very small, at another time very large; for the mind has the power of projecting the images on the retina towards the exterior. Hence the mental field of vision is very small when the sphere of the action of the mind is limited by impediments near the eye: on the contrary, it is very extensive when the projection of the images on the retina towards the exterior, by the influence of the mind, is not impeded. It is very small when we look into a hollow body of small capacity held before the eyes; large when we look out upon a landscape through a small opening; more extensive when we look at the landscape through a window; and most so when our view is not confined by any near object. In all these cases the idea which we receive of the size of the field of vision is very different, although its absolute size is in all the same, being dependent on the extent of the retina. Hence it follows, that the mind is constantly co-operating in the acts of vision, so that at last it becomes difficult to say what belongs to mere sensation, and what to the influence of the mind.

By a mental operation of this kind, we obtain a correct idea of the size of individual objects, as well as of the extent of the field of vision. To understand this, it will be necessary to refer again to fig. 56, p. 553.

The angle $x$, included between the decussating central rays of two cones of light issuing from different points of an object, is called the optical angle—*angulus opticus seu visorius*. This angle becomes larger, the greater the distance between the points A and B; and since the angles $x$ and $y$ are equal, the distance between the points $a$ and $b$ in the image on the retina increases as the angle $x$ becomes larger. Objects at different distances from the eye, but having the same optical angle, $x$—for example, the objects, $c$, $d$, and $e$,—must also throw images of equal size upon the retina; and, if they occupy the same

angle of the field of vision, their image must occupy the same spot in the retina.

Nevertheless, these images appear to the mind to be of very unequal size when the ideas of distance and proximity come into play; for, from the image *a b*, the mind forms the conception of a visual space extending to *e*, *d*, or *c*, and of an object of the size which that represented by the image on the retina appears to have when viewed close to the eye, or under the most usual circumstances. A landscape depicted on the retina, as *a b*, and viewed under the angle *x*, is therefore conceived by the mind to have an extent of two miles perhaps, if we know that its extent is such, or if we infer it to be so from the number of known objects seen at the same time. And in the same way that the images of several different objects, viewed under the same angle, thus appear to the mind to have a different size in the field of vision, so the whole field of vision, which has always the same absolute size, is interpreted by the mind as of extremely various extent; and, for this reason also, the image viewed in the camera obscura is regarded as a real landscape—as the true field of vision—although only a small image depicted upon paper. The same mental process gives rise to the idea of depth in the field of vision; this idea being fixed in our mind principally by the circumstance that, as we ourselves move forwards, different images in succession become depicted on our retina, so that we seem to pass between these images, which to the mind is the same thing as passing between the objects themselves.

The action of the sense of vision in relation to external objects is, therefore, quite different from that of the sense of touch. The objects of the latter sense are immediately present to it; and our own body, with which they come into contact, is the measure of their size. The part of a table touched by the hand appears as large as the part of the hand receiving an impression from it, for a part of our body in which a sensation is excited is here the measure by which we judge of the magnitude of the object. In the sense of vision, on the

contrary, the images of objects are mere fractions of the objects themselves realized upon the retina, the extent of which remains constantly the same. But the imagination which analyzes the sensations of vision, invests the images of objects, together with the whole field of vision, in the retina, with very varying dimensions; the relative size of the images in proportion to the whole field of vision, or of the affected parts of the retina to the whole retina, alone remaining unaltered.

The direction in which an object is seen, the *direction of vision*, or *visual direction*, depends on the part of the retina which receives the image, and on the distance of this part from, and its relation to, the central point of the retina. Thus, objects of which the images fall upon the same parts of the retina lie in the same visual direction; and when, by the action of the mind, the images or affections of the retina are projected into the exterior world, the relation of the images to each other remains the same.

The estimation of the *form of bodies* by sight is the result partly of the mere sensation, and partly of the association of ideas. Since the form of the images perceived by the retina depends wholly on the outline of the part of the retina affected, the sensation alone is adequate to the distinction of only superficial forms from each other, as of a square from a circle. But the idea of a solid body, as a sphere, or a body of three or more dimensions, *e. g.*, a cube, can only be attained by the action of the mind constructing it from the different superficial images seen in different positions of the eye with regard to the object; and, as shewn by Mr. Wheatstone and illustrated in the stereoscope, from two different perspective projections of the body being presented simultaneously to the mind by the two eyes. Hence, when in adult age sight is suddenly restored to persons blind from infancy, all objects in the field of vision appear at first as if painted flat on one surface; and no idea of solidity is formed until after long exercise of the sense of vision combined with that of touch.

We judge of the *motion* of an object, partly from the motion of its image over the surface of the retina, and partly from the motion of our eyes following it. If the image upon the retina moves while our eyes and our body are at rest, we conclude that the object is changing its relative position with regard to ourselves. In such a case the movement of the object may be apparent only, as when we are standing upon a body which is in motion, such as a ship. If, on the other hand, the image does not move with regard to the retina, but remains fixed upon the same spot of that membrane, while our eyes follow the moving body, we judge of the motion of the object by the sensation of the muscles in action to move the eye. If the image moves over the surface of the retina while the muscles of the eye are acting at the same time in a manner corresponding to this motion as in reading, we infer that the object is stationary, and we know that we are merely altering the relation of our eyes to the object. Sometimes the object appears to move when both object and eye are fixed, as in vertigo.

The mind can, by the faculty of *attention*, concentrate its activity more or less exclusively upon the senses of sight, hearing, and touch alternately. When exclusively occupied with the action of one sense, it is scarcely conscious of the sensations of the others. The mind, when deeply immersed in contemplations of another nature, is indifferent to the actions of the sense of sight, as of every other sense. We often, when deep in thought, have our eyes open and fixed, but see nothing, owing to the action of the fibres of the optic nerves being unable to excite the mind to perception when otherwise engaged. The attention which is thus necessary for vision, is necessary also to analyse what the field of vision presents. The mind does not perceive all the objects presented by the field of vision at the same time with equal acuteness, but directs itself first to one and then to another. The sensation becomes more intense, according as the particular object is at the time the

principal subject of mental contemplation. Any compound mathematical figure produces a different impression according as the attention is directed exclusively to one or the other part of it. Thus, in fig. 57, we may in succession have a vivid perception of the whole, or of distinct parts only; of the six triangles near the outer circle, of the hexagon in the middle, or of the three large triangles. The more numerous and varied the parts of which a figure is composed, the more scope does it afford for the play of the attention. Hence it is that architectural ornaments have an enlivening effect on the sense of vision, since they afford constantly fresh subject for the action of the mind.

*Fig.* 57.

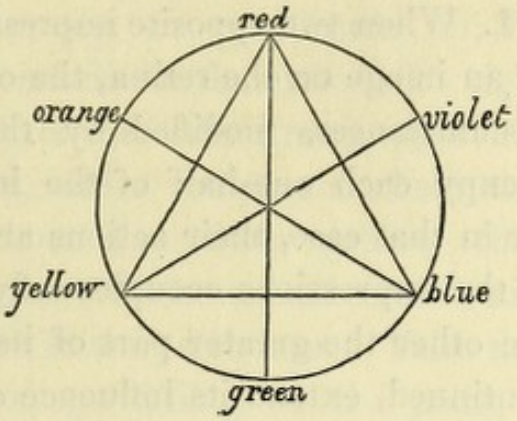
The *duration of the sensations* of the retina is much longer than that of the impressions which produce them: according to Plateau, the sensation persists 0·32 to 0·35 of a second after the impression has ceased; and the duration of the *after-sensation* or *spectrum*, is greater in a direct ratio with the duration of the impression which caused it. Hence the image of a bright object, as of the panes of a window through which the light is shining, may be perceived in the retina for a considerable period, if we have previously kept our eye fixed for some time on it.

The colour of the spectrum varies with that of the object which produced it. The spectra left by the images of white or luminous objects, are ordinarily white or luminous; those left by dark objects are dark. Sometimes, however, the relation of the light and dark parts in the image may, under certain circumstances, be reversed in the spectrum; what was bright may be dark, and what was dark may appear light. This occurs whenever the eye, which is the seat of the spectrum of a luminous object, is not closed, but fixed upon another bright or white surface, as a white wall, or a sheet of white paper. Hence the spectrum of the sun, which, while light is excluded from the eye, is luminous, appears black or grey when the eye is directed upon a white surface. The explanation of this is,

that the part of the retina which has received the luminous image, remains for a certain period afterwards in an excited state, while that which has received a dark image is in an unexcited, and therefore much more excitable, condition.

The ocular spectra which remain after the impression of coloured objects upon the retina, are always coloured; and their colour is not that of the object, or of the image produced directly by the object, but the opposite, or complemental colour. The spectrum of a red object is, therefore, green; that of a green object, red; that of violet, yellow; that of yellow, violet, and so on. The colours which thus reciprocally excite each other in the retina, are those placed at opposite points of the circle in fig. 58.

*Fig.* 58.*




*Of the reciprocal Action of different Parts of the Retina on each other.*

Although each elementary part of the retina represents a distinct portion of the field of vision, yet the different elementary parts, or sensitive points, of that membrane have a certain influence on each other; the particular condition of one influencing that of another, so that the image perceived by one

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* Fig. 58. A circle showing the various simple and compound colours of light, and those which are complemental of each other, *i.e.*, which, when mixed, produce a neutral grey tint. The three simple colours, red, yellow, and blue, are placed at the angles of an equilateral triangle, which are connected together by means of a circle; the mixed colours, green, orange, and violet, are placed intermediate between the corresponding simple or homogeneous colours; and the complemental colours,

part is modified by the image depicted in the other. The phenomena, which result from this relation between the different parts of the retina, may be arranged in two classes; the one including those where the condition existing in the greater extent of the retina is imparted to the remainder of that membrane; the other consisting of those in which the condition of the larger portion of the retina, excites in the less extensive portion, the opposite condition.

1. When two opposite impressions occur in contiguous parts of an image on the retina, the one impression is, under certain circumstances, modified by the other. If the impressions occupy each one-half of the image, this does not take place; for in that case, their actions are equally balanced. But if one of the impressions occupies only a small part of the retina, and the other the greater part of its surface, the latter may, if long continued, extend its influence over the whole retina, so that the opposite less extensive impression is no longer perceived, and its place becomes occupied by the same sensation as the rest of the field of vision. Thus, if we fix the eye for some time upon a strip of coloured paper lying upon a white surface, the image of the coloured object, especially when it falls on the lateral parts of the retina, wlll gradually disappear, and the white surface be seen in its place.

The disappearance of images which fall on the point of entrance of the optic nerve is also attributed by Müller to this property possessed by the retina, of imparting the condition

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of which the pigments, when mixed, would constitute a grey, and of which the prismatic spectra would together produce a white light, will be found to be placed in each case opposite to each other, but connected by a line passing through the centre of the circle. The figure is also useful, in showing the further shades of colour which are complementary of each other. If the circle be supposed to contain every transition of colour between the six marked down, those which, when united, yield a white or grey colour, will always be found directly opposite to each other; thus, for example, the intermediate tint between orange and red is complemental of the middle tint between green and blue.

affecting its larger part to the remainder. The more common explanation of the phenomenon, however, is, that the retina corresponding to the point of entrance of the optic nerve is completely insensible to the impressions of light. The phenomenon itself is very readily shown. If we direct one eye, the other being closed, upon a point at such a distance to the side of any object, that the image of the latter must fall upon the retina at the point of entrance of the optic nerve, this image is lost either instantaneously, or very soon. If, for example, we close the left eye, and direct the axis of the right eye steadily towards the circular spot here represented, while the page is held at a distance about five times greater than that of the objects from each other, the cross will vanish, and the colour of the paper will be seen in its place. That this phenomenon arises from the image falling on the point of entrance of the optic nerve, is shown by fixing the same eye upon the cross instead of upon the round dot; the latter object then does not disappear, or only after long persistence of the impression.

2. In the second class of phenomena, the affection of one part of the retina influences that of another part not in such a manner as to obliterate it, but so as to cause it to become the contrast or opposite of itself. Thus a grey spot upon a white ground appears darker than the same tint of grey would do if it alone occupied the whole field of vision, and a shadow is always rendered deeper when the light which gives rise to it becomes more intense, owing to the greater contrast. The former phenomena ensue gradually, and only after the images have been long fixed on the retina; the latter are instantaneous in their production, and are permanent.

In the same way, also, colours may be produced by contrast. Thus, a very small dull-grey strip of paper, lying upon an extensive surface of any bright colour, does not appear grey, but has a faint tint of the colour which is the contrast of that of the surrounding surface (see page 561). A strip of grey paper

upon a green field, for example, often appears to have a tint of red, and when lying upon a red surface, a greenish tint; it has an orange-coloured tint upon a bright blue surface, and a blueish tint upon an orange-coloured surface; a yellowish colour upon a bright violet, and a violet tint upon a bright yellow surface. The colour excited thus, as a contrast to the exciting colour, being wholly independent of any rays of the corresponding colour acting from without upon the retina, must arise as an opposite or antagonistic condition of that membrane; and the opposite conditions of which the retina thus becomes the subject would seem to balance each other by their reciprocal reaction. A necessary condition for the production of the contrasted colours is, that the part of the retina in which the new colour is to be excited, shall be in a state of comparative repose; hence the small object itself must be grey. A second condition is, that the colour of the surrounding surface shall be very bright, that is, it shall contain much white light.

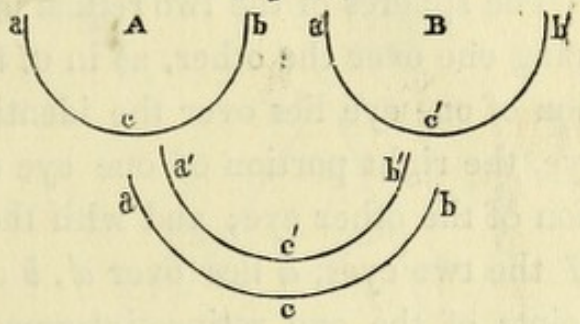
### *Of the Simultaneous Action of the two Eyes.*

Although the sense of sight is exercised by two organs, yet the impression of an object conveyed to the mind is single. Various theories have been advanced to account for this phenomenon. By Gall, it was supposed that we do not really employ both eyes simultaneously in vision, but always see with only one at a time. This especial employment of one eye in vision certainly occurs in persons whose eyes are of very unequal focal distance, but in the majority of individuals both eyes are simultaneously in action in the perception of the same object; this is shewn by the double images seen under certain conditions. If two fingers be held up before the eyes, one in front of the other, and vision be directed to the more distant, so that it is seen singly, the nearer will appear double; while if the nearer one be regarded, the more distant will be

seen double; and one of the double images in each case will be found to belong to one eye, the other to the other eye.

Single vision results only when certain parts of the two retinæ are affected simultaneously; if different parts of the retinæ receive the image of the object, it is seen double. The parts of the retinæ in the two eyes which thus correspond to each other in the property of referring the images which affect them simultaneously, to the same spot in the field of vision, are in man just those parts which would correspond to each other if one retina were placed exactly in front of, and over, the other (as in fig. 59, c). Thus the outer lateral portion of one eye corresponds to, or, to use a better term, is identical with, the inner portion of the other eye; or *a* of the eye A (fig. 59) with *a'* of the eye B. The upper part of one retina is also identical with the upper part of the other; and the lower parts of the two eyes are identical with each other.

*Fig* 59.




This is proved by a single experiment. Pressure upon any part of the ball of the eye, so as to affect the retina, produces a luminous circle seen at the opposite side of the field of vision to that on which the pressure is made. If, now, in a dark room, we press with the finger at the upper part of one eye, and at the lower part of the other, two luminous circles are seen, one above the other, so, also, two figures are seen, when pressure is made simultaneously on the two outer or the two inner sides of both eyes. It is certain, therefore, that neither the upper part of one retina and the lower part of the other are identical, nor the outer lateral parts of the two retinæ, nor their inner lateral portions. But if pressure be made with the fingers upon both eyes simultaneously at their lower part, one luminous ring is seen at the middle of the upper part of the

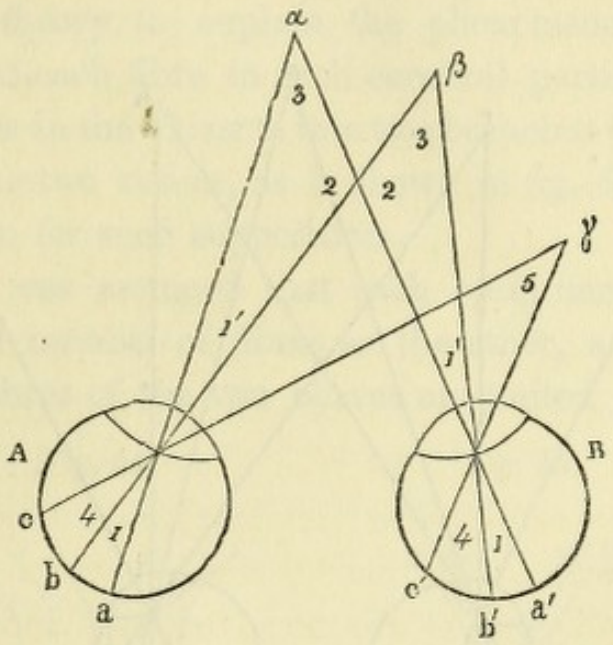
field of vision; if the pressure be applied to the upper part of both eyes, a single luminous circle is seen in the middle of the field of vision below. So, also, if we press upon the outer side *a* of the eye A, and upon the inner side *a'* of the eye B, a single spectrum is produced, and is apparent at the extreme right of the field of vision; if upon the point *b* of one eye, and the point *b'* of the other, a single spectrum is seen to the extreme left.

The spheres of the two retinæ may, therefore, be regarded as lying one over the other, as in C, fig. 59; so that the left portion of one eye lies over the identical left portion of the other eye, the right portion of one eye over the identical right portion of the other eye; and with the upper and lower portions of the two eyes, *a* lies over *a'*, *b* over *b'*, and *c* over *c'*. The points of the one retina intermediate between *a* and *c*, are again identical with the correspondent points of the other retina between *a'* and *c'*; those between *b* and *c* of the one retina, with those between *b'* and *c'* of the other. In short, all other parts are non-identical: and, when they are excited to action, the effect is the same as if the impressions were made on different parts of the same retina: and the double images belonging to the eyes A and B, are seen at exactly the same distance from each other as exists between the image of the eye A and the part of the retina of the eye A which corresponds to, or is identical with, the seat of the second image in the eye B; or, to return to the figure already used in illustration (fig. 59), if *a* of one eye be affected, and *b'* of the other, the distances of the two images *a* and *b'* will, inasmuch as *a* is identical with *a'*, and *b* with *b'*, lie at exactly the same distance from each other as images produced by impressions on the points *a b* of the one eye, or *a' b'* of the other.

In application of these results to the phenomena of vision, if the position of the eyes with regard to a luminous object be such that similar images of the same object fall on identical parts of the two retinæ, as occurs when the axes meet in some one point, the object is seen single; if otherwise, as in the

various forms of squinting, two images are formed, and double vision results. If the axes of the eyes, A and B (fig. 60), be so directed that they meet at *a*, an object at *a* will be seen singly, for the point *a* of the one retina, and *a'* of the other, are identical. So, also, if the object $\beta$ be so situated that its image falls in both eyes at the same distance from the central point of the retina,— namely, at *b* in the one eye, and at *b'* in the other, —$\beta$ will be seen single, for it affects identical parts of the two retinæ. The same will apply to the object $\delta'$.

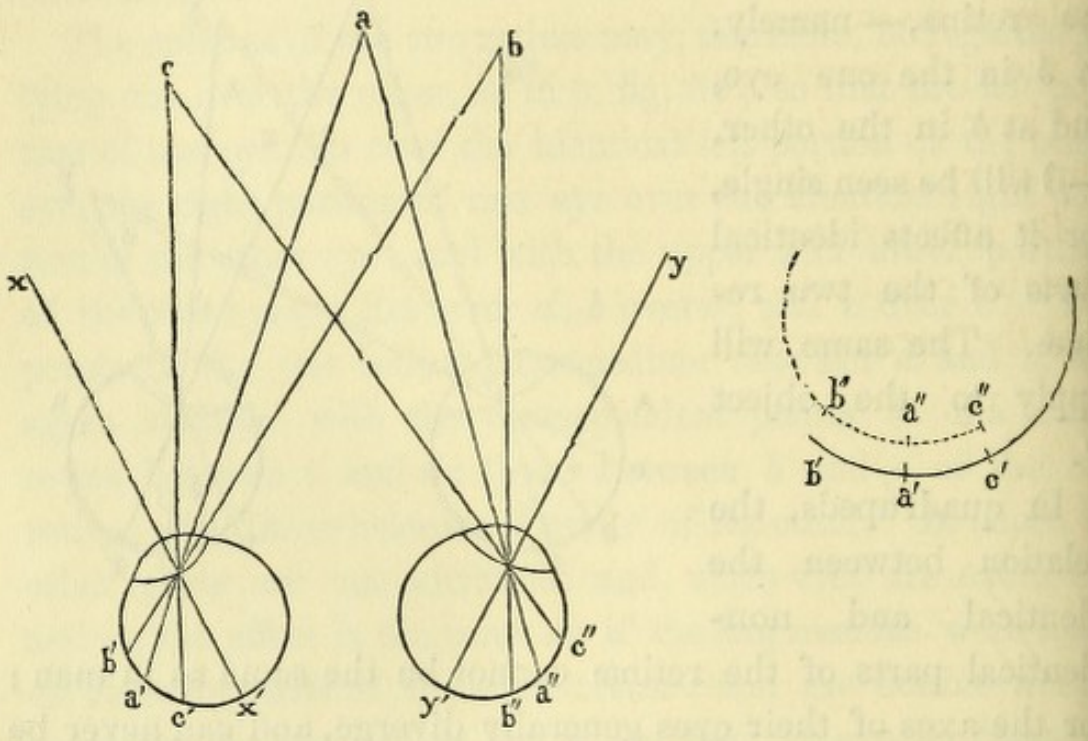
*Fig.* 60.




In quadrupeds, the relation between the identical and non-identical parts of the retinæ cannot be the same as in man; for the axes of their eyes generally diverge, and can never be made to meet in one point of an object. When an animal regards an object situated directly in front of it, the image of the object must fall, in both eyes, on the outer portion of the retinæ. Thus the image of the object *a* (fig. 61) will fall at *a'* in one eye, and at *a''* in the other: and these points *a'* and *a''* must be identical. So, also, for distinct and single vision of objects, *b* or *c*, the points *b'* and *b''*, or *c' c''*, in the two retinæ, on which the images of these objects fall, must be identical. All points of the retina in each eye which receive rays of light from lateral objects only, can have no correspondent identical points in the retina of the other eye; for otherwise two objects, one situated to the right and the other to the left, would appear to lie in the same spot of the field of vision. It is probable, therefore, that there are in the eyes of animals

parts of the retinæ which are identical, and parts which are not identical, *i.e.*, parts in one which have no corresponding parts in the other eye. And the relation of the two retinæ to each other in the field of vision may be represented as in fig. 62.

*Fig.* 61. *Fig.* 62.



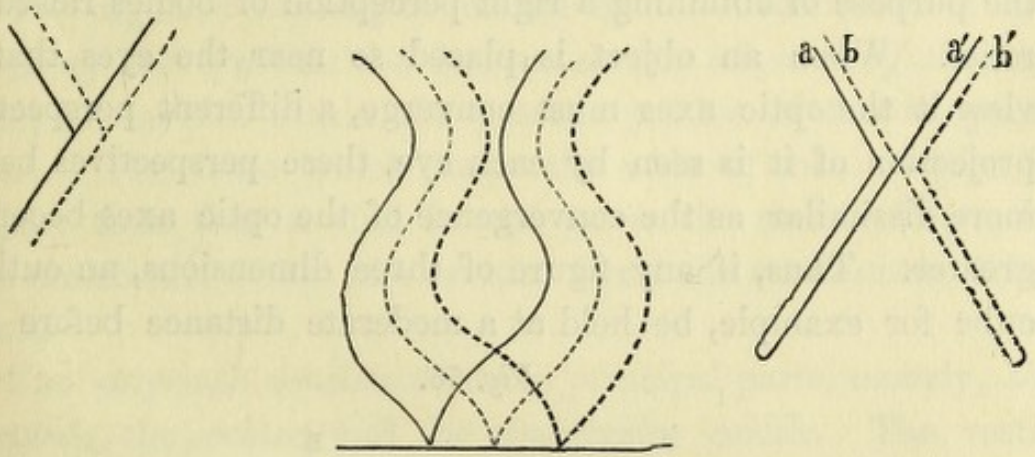

The cause of the impressions on identical points of the two retinæ giving rise to but one sensation, and the perception of a single image, must either lie in the structural organization of the deeper or cerebral portion of the visual apparatus, or be the result of a mental operation; for in no other case is it the property of the corresponding nerves of the two sides of the body to refer their sensations as one to one spot.

Many attempts have been made to explain this remarkable relation between the eyes, by referring it to anatomical relations between the optic nerves. The circumstance of the inner portion of the fibres of the two optic nerves decussating at the commissure, and passing to the eye of the opposite side, while the outer portion of the fibres continue their course to the eye

of the same side, so that the left side of both retinæ is formed from one root of the nerves, and the right side of both retinæ from the other root, naturally led to an attempt to explain the phenomenon by this distribution of the fibres of the nerves. And this explanation is favoured by cases in which the entire of one side of the retina, as far as the central point in both eyes, sometimes becomes insensible. But Müller shews the inadequateness of this theory to explain the phenomenon, unless it be supposed that each fibre in each cerebral portion of the optic nerves divides in the chiasma into two branches for the identical points of the two retinæ, as is shewn in fig. 63. But there is no foundation for such supposition.

By another theory it was assumed that each optic nerve contains exactly the same number of fibres as the other, and that the correspondent fibres of the two nerves are united in

*Fig.* 63. *Fig.* 64. *Fig.* 65.



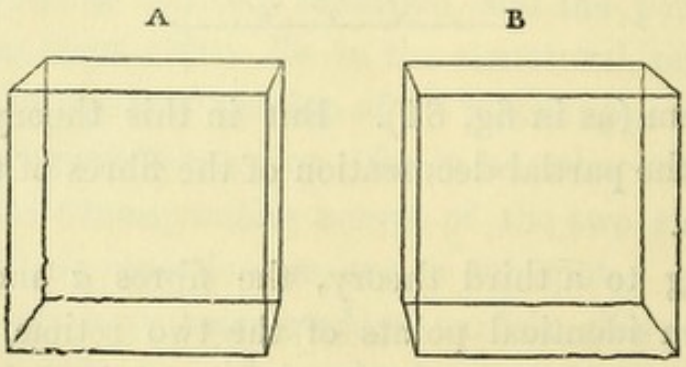

the sensorium (as in fig. 64). But in this theory no account is taken of the partial decussation of the fibres of the nerves in the chiasma.

According to a third theory, the fibres *a* and *a′*, fig. 65, coming from identical points of the two retinæ, are in the chiasma brought into one optic nerve, and in the brain either are united by a loop, or spring from the same point. The same disposition prevails in the case of the identical fibres *b* and *b′*. According to this theory, the left half of each retina would be represented in the left hemisphere of the brain, and the right half of each retina in the right hemisphere.

Another explanation is founded on the fact, that at the anterior part of the chiasma of the optic nerve, certain fibres pass across from the distal portion of one nerve to the corresponding portion of the other nerve, as if they were commisural fibres forming a connection between the retinæ of the two eyes. It is supposed, indeed, that these fibres may connect the corresponding parts of the two retinæ, and may thus explain their unity of action; in the same way as corresponding parts of the cerebral hemispheres are believed to be connected together by the commisural fibres of the corpus callosum, and so enabled to exercise unity of function.

But, on the whole, it is more probable, that the power of forming a single idea of an object from a double impression conveyed by it to the eye is the result of a mental act. This is supported by the same facts as those, by which the power has been shewn by Professor Wheatstone to be subservient to the purpose of obtaining a right perception of bodies raised in relief. When an object is placed so near the eyes that to view it the optic axes must converge, a different perspective projection of it is seen by each eye, these perspectives being more dissimilar as the convergence of the optic axes becomes greater. Thus, if any figure of three dimensions, an outline cube for example, be held at a moderate distance before the

*Fig.* 66.




eyes, and viewed with each eye successively, while the head is kept perfectly steady, A (fig. 66) will be the picture presented to the right eye, and B that seen by the left eye. Mr. Wheatstone has shown that on this circumstance depends in a great

measure our conviction of the solidity of an object, or of its projection in relief. If different perspective drawings of a solid body, one representing the image seen by the right eye, the other that seen by the left (for example, the drawing of a cube A, B, fig. 66), be presented to corresponding parts of the two retinæ, as may be readily done by means of the *stereoscope*, an instrument invented by Professor Wheatstone for the purpose, the mind will perceive not merely a single representation of the object, but a body projecting in relief, the exact counterpart of that from which the drawings were made.

## SENSE OF HEARING.

### *Anatomy of the Organ of Hearing.*

The organ of hearing is formed by the distribution of the auditory nerve within the *internal ear*, or *labyrinth of the ear*, a set of cavities within the petrous portion of the temporal bone. The bone which forms the walls of these cavities is denser than that around it, and forms the *osseous labyrinth;* the membrane within the cavities forms the *membranous labyrinth.*

The labyrinth consists of three principal parts, namely, *the vestibule,* the *cochlea*, and the *semicircular canals.* The vestibule is the middle cavity of the labyrinth, and the central organ of the whole auditory apparatus. It presents, in its inner wall, several openings for the entrance of the divisions of the auditory nerve; in its outer wall, the *fenestra ovalis*, an opening filled by the base of the *stapes*, one of the small bones of the ear; in its posterior and superior walls, five openings by which the *semicircular canals* communicate with it: in its anterior wall, an opening leading into the *cochlea.* The hinder part of the inner wall of the vestibule also presents an opening, the orifice of the *aquæductus vestibuli*, a canal leading to the posterior margin of the petrous bone, with uncertain contents and unknown purpose.

The *semicircular canals* are six arched cylindriform bony canals, set in the substance of the petrous bone. They all open at both ends into the vestibule (two of them first coalescing). The ends of each are dilated just before opening into the vestibule; and one end of each being more dilated than the other is called an *ampulla*. Two of the canals form nearly vertical arches; of these the superior is also anterior; the posterior is inferior; the third canal is horizontal, and lower and shorter than the others.

The *cochlea*, a small organ, shaped like a common snail-shell, is seated in front of the vestibule, its base resting on the bottom of the internal meatus, where some apertures transmit to it the cochlear filament of the auditory nerve. In its axis the cochlea is traversed by a conical column or *modiolus*, around which a *spiral canal* winds with about two turns and a half from the base to the apex. At the apex of the cochlea the canal is closed; at the base it presents three openings, of which one, already mentioned, communicates with the vestibule; another, called *fenestra rotunda*, is separated by a membrane from the cavity of the tympanum; the third is the orifice of the *aquæductus cochleæ*, a canal leading to the jugular fossa of the petrous bone, and corresponding, at least in obscurity of purpose and origin, to the aquæductus vestibuli. The spiral canal is divided into two passages, or *scalæ*, by a partition of bone and membrane, the *lamina spiralis*. The osseous part or *zone* of this lamina, is connected with the modiolus; the membranous part, with a muscular zone forming its outer margin, is attached to the outer wall of the canal.* Commencing at the base of the cochlea, between its vestibular and tympanic openings, they form a partition between these apertures; the two scalæ are, therefore, in correspondence with this arrangement, named *scala vestibuli* and *scala tympani*. At the apex of the cochlea, the lamina spiralis ends in a small *hamulus*, the

* A very minute description of the structure of the *lamina spiralis*, and *cochlearis muscle* is given in Todd and Bowman's Physiological Anatomy of Man.

inner and concave part of which, being detached from the summit of the modiolus, leaves a small aperture by which the two scalæ, separated in all the rest of their length, communicate.

Within the cavities now described is the *membranous labyrinth*, which corresponds generally with their form, but is separated from the walls of the vestibule and semicircular canals, except where the nerves enter into connection within it. The membranous labyrinth contains a fluid called *endolymph*; and between its outer surface and the inner surface of the walls of the vestibule and semicircular canals is another collection of similar fluid called *perilymph*: so that all the sonorous vibrations impressing the auditory nerves on these parts of the internal ear are conducted through fluid to a membrane suspended in and containing fluid. The fluid in the cochlea communicates with that in the vestibule, but there is no fluid external to its lining membrane.

The vestibular portion of the membranous labyrinth comprises two, probably communicating, cavities, of which the upper and larger is named the *utriculus*; the lower the *sacculus*. In the former open the orifices of the membranous semicircular canals. The membrane composing this labyrinth is laminated, transparent, very vascular, covered on both surfaces with nucleated cells; in the cavities which it encloses, especially in the utriculus and sacculus, it contains small masses of calcareous particles, *otoconia* or *ear-powder*.

The *auditory nerve*, for the appropriate exposure of whose filaments to sonorous vibrations all the organs now described are provided, is characterized as a nerve of special sense by its softness (whence it derived its name of *portio mollis* of the seventh pair), and by the fineness of its component fibres. It enters the labyrinth of the ear in two divisions: one for the vestibule and semicircular canals, and the other for the cochlea. The branches for the vestibule spread out and radiate on the inner surface of the membranous labyrinth, and appear to mingle with the calcareous powder: their exact termination is

unknown. Those for the semicircular canals pass into the ampullæ, and form, within each of them, a bulging projection, in which according to Wagner, they terminate in free loops. The branches for the cochlea enter it through orifices at the base of the modiolus, which they ascend, and thence successively pass into canals in the osseous part of the lamina spiralis. In the canals of this osseous part or zone, the nerves are arranged in plexuses; and beyond them, entering the membranous part of the lamina, they terminate either in free extremities or in loops; according to Corti and others many of them end in nerve-corpuscles.

Such are the essential parts of the human organ of hearing. To these, others are adapted for the proper transmission of the sonorous vibrations of the air through, chiefly the fenestra rotunda and the fenestra ovalis, the apertures by which the internal ear is separated by membrane alone from the cavity of the *tympanum* or *middle ear*. The tympanum is an air-cavity in the temporal bone, opening through its anterior and inner wall into the Eustachian tube, a cylindriform flattened canal, dilated at both ends, composed partly of bone and partly of cartilage, lined with mucous membrane, and forming a communication between the tympanum and the pharynx. It opens into the cavity of the pharynx just behind the posterior aperture of the nostrils. The cavity of the tympanum communicates with the air-cavities in the mastoid process of the temporal bone; but its only opening to the external air is through the Eustachian tube. The walls of the tympanum are osseous, except where apertures in them are closed with membrane as at the fenestra rotunda, and fenestra ovalis, and at the outer part where the bone is replaced by the *membrana tympani*. The cavity of the tympanum is lined with mucous membrane and ciliated epithelium continuous with that of the pharynx. It contains a chain of small bones (*ossicula auditus*), which extends from the membrana tympani to the fenestra ovalis.

The *membrana tympani* is placed in a slanting direction at the bottom of the external auditory canal, its plane being at

an angle of about 45° with the lower wall of the canal. It is formed chiefly, of a tough and tense fibrous membrane, the edges of which are set in a bony groove; its outer surface is covered with a continuation of the epidermal lining of the auditory canal, its inner surface, with part of the ciliated mucous membrane of the tympanum.

The *ossicles* of the ear are three, named *malleus*, *incus*, and *stapes*. The *malleus*, or hammer-bone, is attached by a long slightly-curved process, called its handle, to the membrana tympani; the line of attachment being vertical, including the whole length of the handle, and extending from the upper border to the centre of the membrane. The head of the malleus is irregularly rounded; its neck, or the line of boundary between it and the handle, supports two processes: a *short* conical one, which receives the insertion of the *tensor tympani*, and a *slender* one, *processus gracilis*, which extends forwards, and to which the *laxator tympani* muscle is attached. The *incus*, or anvil-bone, shaped like a biscuspid molar tooth, is articulated by its broader part, corresponding with the surface of the crown of a tooth, to the malleus. Of its two fang-like processes, one, directed backwards, has a free end; the other, curved downwards and more pointed, articulates with the *stapes*, a little bone shaped exactly like a stirrup, of which the base or bar fits in the fenestra ovalis. To the neck of the stapes, a short process, corresponding with the loop of the stirrup, is attached the *stapedius* muscle.

The bones of the ear are covered with mucous membrane reflected over them from the wall of the tympanum; and are moveable both altogether and one upon the other. The malleus moves and vibrates with every movement and vibration of the membrana tympani, and its movements are communicated through the incus to the stapes, and through it to the membrane closing the fenestra ovalis. The malleus, also, is moveable in its articulation with the incus; and the membrana tympani moving with it is altered in its degree of tension by the laxator and tensor tympani muscles. The stapes is moveable

on the process of the incus, when the stapedius muscle acting draws it backwards.

The external ear consists of the *auricle* and external *auditory canal.* The principal parts of the auricle are two prominent rims enclosed one within the other (*helix* and *anthelix*), and enclosing a central hollow named the *concha ;* in front of the concha, a prominence directed backwards, the *tragus*, and opposite to this, one directed forwards, the *antitragus.* From the concha, the auditory canal, with a slight arch directed upwards, passes inwards and a little forwards to the membrana tympani, to which it thus serves to convey the vibrating air. Its outer part consists of fibro-cartilage continued from the concha; its inner part of bone.

### *Physiology of Hearing.*

The acoustic portion of the physiology of hearing is thus illustrated by Müller: chiefly in applications of the results of his experiments on the conduction of sonorous vibrations through various combinations of air, water, and solid substances, especially membrane.

All the acoustic contrivances of the organ of hearing are means for conducting the sound, just as the optical apparatus of the eye are media for conducting the light. Since all matter is capable of propagating sonorous vibrations, the simplest conditions must be sufficient for mere hearing; for all substances surrounding the auditory nerve would communicate sound to it. In the eye a certain construction was required for directing the rays or undulations of light in such a manner that they should fall upon the optic nerve with the same relative disposition as that with which they issued from the object. In the sense of hearing this is not requisite. Sonorous vibrations, having the most various direction and the most unequal rate of succession, are transmitted by all media without modification, however manifold their decussations; and, wherever these vibrations or undulations fall upon the organ of hearing

and the auditory nerves, they must cause the sensation of corresponding sounds. The whole development of the organ of hearing, therefore, can have for its object merely the *rendering more perfect* the propagation of the sonorous vibrations, and their *multiplication* by resonance; and, in fact, all the acoustic apparatus of the organ may be shown to have reference to these two principles.

### *Functions of the External Ear.*

The external auditory passage influences the propagation of sound to the tympanum in three ways: 1, by causing the sonorous undulations, entering directly from the atmosphere, to be transmitted by the air in the passage immediately to the membrana tympani, and thus preventing them from being dispersed; 2, by the walls of the passage conducting the sonorous undulations imparted to the external ear itself, by the shortest path to the attachment of the membrana tympani, and so to this membrane; 3, by the resonance of the column of air contained within the passage.

As a conductor of undulations of air, the external auditory passage receives the direct undulations of the atmosphere, of which those that enter in the direction of its axis produce the strongest impressions. The undulations which enter the passage obliquely are reflected by its parietes, and thus by reflexion reach the membrana tympani. By reflexion, also, the external meatus receives the undulations which impinge upon the concha of the external ear, when their angle of reflexion is such that they are thrown towards the tragus. Other sonorous undulations, again, which could not enter the meatus from the external air either directly or by reflexion, may still be brought into it by inflexion; undulations, for instance, whose direction is that of the long axis of the head, and which pass over the surface of the ear, must, in accordance with the laws of inflexion, be bent into the external meatus by its margins.

But the action of those undulations which enter the meatus directly are most intense; and hence we are enabled to judge of the point whence sound comes, by turning one ear in different directions, till it is directed to the point whence the vibrations may pass directly into the meatus, and produce the strongest impressions.

The walls of the meatus are also solid conductors of sound; for those vibrations which are communicated to the cartilage of the external ear, and not reflected from it, are propagated by the shortest path through the parietes of the passage to the membrana tympani. Hence, both ears being close stopped, the sound of a pipe is heard more distinctly when its lower extremity, covered with a membrane, is applied to the cartilage of the external ear itself, than when it is placed in contact with the surface of the head.

Lastly, the external auditory passage is important, inasmuch as the air which it contains, like all insulated masses of air, increases the intensity of sounds by resonance. To convince ourselves of this, we need only lengthen the passage by affixing to it another tube: every sound that is heard, even the sound of our own voice, is then much increased in intensity.

The action of the cartilage of the external ear upon sonorous vibrations is partly to reflect them, and partly to condense and conduct them to the parietes of the external passage. With respect to its reflecting action, the concha is the most important part, since it directs the reflected undulations towards the tragus, whence they are reflected into the auditory passage. The other inequalities of the external ear do not promote hearing by reflection; and, if the conducting power of the cartilage of the ear were left out of consideration, they might be regarded as destined for no particular use; but receiving the impulses of the air, the cartilage of the external ear, while it reflects a part of them, propagates within itself and condenses the rest, as all other solid and elastic bodies

would do. Thus, the sonorous vibrations which it receives by an extended surface, are conducted by it to its place of attachment. In consequence of the connection of the parietes of the auditory passage with the solid parts of the whole head, some dispersion of the undulations will result; but the points of attachment of the membrana tympani will receive them by the shortest path, and will as certainly communicate them to that membrane, as the solid sides of a drum communicate sonorous undulations to the parchment head, or the bridge of a musical string, its vibrations to the string.

Regarding the cartilage of the external ear, therefore, as a conductor of sonorous vibrations, all its inequalities, elevations, and depressions, which are useless with regard to reflexion, become of evident importance; for those elevations and depressions upon which the undulations fall perpendicularly, will be affected by them in the most intense degree; and, in consequence of the various form and position of these inequalities, sonorous undulations, in whatever direction they may come, must fall perpendicularly upon the tangent of some one of them. This affords an explanation of the extraordinary form given to this part.

## *Functions of the Middle Ear; the Tympanum, Ossicula, and Fenestræ.*

In animals living in the atmosphere, the sonorous vibrations are conveyed to the auditory nerve by three different media in succession; namely, the air, the solid parts of the body of the animal and of the auditory apparatus, and the fluid of the labyrinth.

Sonorous vibrations are imparted too imperfectly from air to solid bodies, for the propagation of sound to the internal ear to be adequately effected by that means alone: yet already an instance of its being thus propagated has been mentioned.

In passing from air directly into water, sonorous vibrations

suffer also a considerable diminution of their strength; but if a tense membrane exists between the air and the water, the sonorous vibrations are communicated from the former to the latter medium with very great intensity. This fact, of which Müller gives experimental proof, furnishes at once an explanation of the use of the fenestra rotunda, and of the membrane closing it. They are the means of communicating, in full intensity, the vibrations of the air in the tympanum to the fluid of the labyrinth. This peculiar property of membranes is the result, not of their tenuity alone, but of the elasticity and capability of displacement of their particles; and it is not impaired, when, like the membrane of the fenestra rotunda, they are not impregnated with moisture.

Sonorous vibrations are also communicated without any perceptible loss of intensity from the air to the water, when to the membrane forming the medium of communication, there is attached a short, solid body, which occupies the greater part of its surface, and is alone in contact with the water. This fact elucidates the action of the fenestra ovalis, and of the plate of the stapes which occupies it: and, with the preceding fact, shows that both fenestræ—that closed by membrane only, and that with which the moveable stapes is connected—transmit very freely the sonorous vibrations from the air to the fluid of the labyrinth.

A small, solid body, fixed in an opening by means of a border of membrane, so as to be moveable, communicates sonorous vibrations, from air on the one side, to water, or the fluid of the labyrinth, on the other side, much better than solid media not so constructed. But the propagation of sound to the fluid is rendered much more perfect if the solid conductor thus occupying the opening, or fenestra ovalis, is by its other end fixed to the middle of a tense membrane, which has atmospheric air on both sides.

A tense membrane is a much better conductor of the vibrations of air than any other solid body bounded by definite surfaces; and the vibrations are also communicated very

readily by tense membranes to solid bodies in contact with them. Thus, then, the membrana tympani serves for the transmission of sound from the air to the chain of auditory bones. Stretched tightly in its osseous ring, it vibrates with the air in the auditory passage, as any thin tense membrane will when the air near it is thrown into vibrations by the sounding of a tuning-fork or a musical string. And, from such a tense vibrating membrane, the vibrations are communicated with great intensity to solid bodies which touch it at any point. If, for example, one end of a flat piece of wood be applied to the membrane of a drum while the other end is held in the hand, vibrations are felt distinctly when the vibrating tuning fork is held over the membrane without touching it; but the wood alone, isolated from the membrane, will only very feebly propagate the vibrations of the air to the hand.

The ossicula of the ear, which are represented in this experiment by the piece of wood, are the better conductors of the sonorous vibrations communicated to them, on account of being isolated by an atmosphere of air, and not continuous with the bones of the cranium; for every solid body thus isolated by a different medium propagates vibrations with more intensity through its own substance than it communicates them to the surrounding medium, which thus prevents a dispersion of the sound; just as the vibrations of the air in the tubes used for conducting the voice from one apartment to another are prevented from being dispersed by the solid walls of the tube. The vibrations of the membrana tympani are transmitted, therefore, by the chain of ossicula to the fenestra ovalis and fluid of the labyrinth, their dispersion in the tympanum being prevented by the difficulty of the transition of vibrations from solid to gaseous bodies. The membrana tympani being a tense, solid body, bounded by free surfaces, the sonorous undulations will be partially reflected at its surfaces, so as to cause a meeting of undulations from opposite directions within it; it will, therefore, by resonance increase the

intensity of the vibrations communicated to it, and the undulations thus rendered more intense will act, in their turn, upon the chain of auditory bones.

The oscillations of the membrana tympani, as a whole, produced by very intense sounds, will, if the undulations of the air fall upon the membrane in a perpendicular direction, occupy its whole extent at once; but if the undulations of the air fall upon it obliquely, so as to strike one part of it before the rest, the movement of the membrane will commence at this point, and will thence extend to the other parts, like the oscillation which is excited near one extremity of a musical string, or at one limited part of the membrane of a drum. These oscillations, being reflected at the borders of the membrane, will traverse it to and fro. In consequence of the oblique position of the membrana tympani, this must always occur when the sonorous undulations enter the ear in the direction of the meatus auditorius externus, that is, in a direction parallel with its axis. When the sonorous undulations enter the meatus in any other direction, they will be reflected backwards and forwards by the walls of the passage; and it will depend on the angles at which they are reflected, in what manner, and at what point, they shall first strike upon the membrana tympani.

The propagation of the undulations of condensation and rarefaction, in which the smaller particles merely of the membrane move, is also modified in the same way by the mode in which the undulations of the air strike it. The undulations of the air either strike every part of its surface simultaneously, or one point of it before the rest: in the latter case, the undulations communicated to the membrane are propagated in it in a determinate direction as far as its border, and then reflected back, so as to give rise to the crossing of undulations in the membrane.

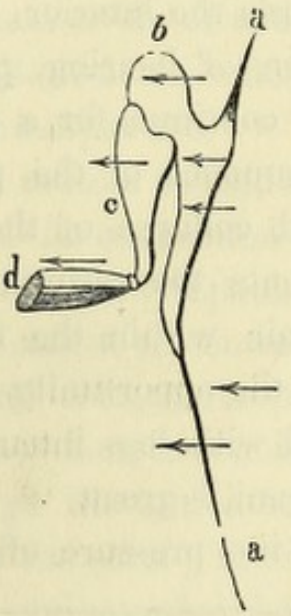
The necessity of the presence of air on the inner side of the membrana tympani in order to enable it and the ossicula auditus to fulfil the objects just described, is obvious. Without this

provision, neither would the vibrations of the membrane be free, nor the chain of bones isolated, so as to propagate the sonorous undulations with concentration of their intensity. But while the oscillations of the membrana tympani are readily communicated to the air in the cavity of the tympanum, those of the solid ossicula will not be conducted away by the air, but will be propagated to the labyrinth without being dispersed in the tympanum. Equally necessary is the communication of the air in the tympanum with the external air through the medium of the Eustachian tube for the maintenance of the equilibrium of pressure and temperature between them.

The propagation of sound through the ossicula of the tympanum to the labyrinth must be effected by undulations of condensation and rarefaction of their particles only, not by oscillations of the entire bones, even in cases where the entire membrana tympani oscillates; for, if the stapes were in its vibrations alternately approximated to and removed from the labyrinth, the fluid of the latter cavity must necessarily be very compressible.*

The long process of the malleus receives the undulations of the membrana tympani (fig. 67, *a*, *a*) and of the air in a direction, indicated by the arrows, nearly perpendicular to itself. From the long process of the malleus they are propagated to its head (*b*); thence into the incus (*c*), the long process of which is parallel with the long process of the malleus. From the long process of the incus the undulations are communicated to the stapes (*d*), which is united to the incus at right angles. These several changes in the direction of the chain of bones have, however, no influence on that of the undulations, which remains the same

*Fig.* 67.




* Edouard Weber (cxxxv. 1846) has shewn, however, that the existence of the membrane over the fenestra rotunda will permit of such

as it was in the meatus externus and long process of the malleus, so that the undulations are communicated by the stapes to the fenestra ovalis in a perpendicular direction.

Increasing tension of the membrana tympani diminishes the facility of transition of sonorous undulations from the air to it. M. Savart observed that the dry membrana tympani, on the approach of a body emitting a loud sound, rejected particles of sand strewn upon it more strongly when lax than when very tense; and inferred, therefore, that hearing is rendered less acute by increasing the tension of the membrana tympani. Müller has confirmed this by experiments with small membranes arranged so as to imitate the membrana tympani: and it may be confirmed also by observations on one's self. For the membrana tympani in one's own person may be rendered tense at will in two ways, namely, by a strong and continued effort of expiration or of inspiration, while the mouth and nostrils are closed. In the first case, the compressed air is forced with a whizzing sound into the tympanum, the membrana tympani is made tense, and immediately hearing becomes indistinct. The same temporary imperfection of hearing is produced by rendering the membrana tympani tense, and convex towards the interior, by the effort of inspiration. The imperfection of hearing, produced by the last-mentioned method, may continue for a time even after the mouth is opened, in consequence of the previous effort at inspiration having induced collapse of the walls of the Eustachian tubes, which prevents the restoration of equilibrium of pressure between the air within the tympanum and that without: hence we have the opportunity of observing that even our own voice is heard with less intensity when the tension of the membrana tympani is great.

If the pressure of the external air or atmosphere be very

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approximation and removal of the stapes to and from the labyrinth. When by the stapes the membrane of the fenestra ovalis is pressed towards the labyrinth, the membrane of the fenestra rotunda may, by the pressure communicated through the fluid of the labyrinth, be pressed towards the cavity of the tympanum.

great, while, on account of collapse of the walls of the Eustachian tube, the air in the interior of the tympanum fails to exert an equal counter pressure, the membrana tympani will of course be forced inwards, and imperfect deafness be produced. Thus it may be explained why, in a diving-bell, voices sound faintly. In all cases, the effect of the increased tension of the membrana tympani is not to render both grave and acute sounds equally fainter than before. On the contrary, as observed by Dr. Wollaston, the increased tension of the membrana tympani produced by exhausting the cavity of the tympanum, makes one deaf to grave sounds only.

The principal office of the Eustachian tube, in Müller's opinion, has relation to the prevention of these effects of increased tension of the membrana tympani. Its existence and openness will provide for the maintenance of the equilibrium between the air within the tympanum and the external air, so as to prevent the inordinate tension of the membrana tympani which would be produced by too great or too little pressure on either side. While discharging this office, however, it will serve to render sounds clearer, as (Henle suggests) the apertures in violins do; to supply the tympanum with air; and to be an out-let for mucus: and the ill effects of its obstruction may be referred to the hindrance of all these its offices, as well as of that one ascribed to it as its principal use.

The influence of the tensor tympani muscle in modifying hearing may also be probably explained in connection with the regulation of the tension of the membrana tympani. If, through reflex nervous action, it can be excited to contraction by a very loud sound, just as the iris and orbicularis palpebrarum muscle are by a very intense light, then, it is manifest that a very intense sound would, through the action of this muscle, induce a deafening or muffling of the ears. In favour of this supposition we have the fact that a loud sound excites, by reflection, nervous action, winking of the eyelids, and, in persons of irritable nervous system, a sudden contraction of many muscles.

The influence of the stapedius muscle in hearing is unknown. It acts upon the stapes in such a manner as to make it rest obliquely in the fenestra ovalis, depressing that side of it on which it acts, and elevating the other side to the same extent.

When the fenestra ovalis and fenestra rotunda exist together with a tympanum, the sound is transmitted to the fluid of the internal ear in two ways,—namely, by solid bodies and by membrane; by both of which conducting media sonorous vibrations are communicated to water with considerable intensity. The sound being conducted to the labyrinth by two paths will, of course, produce so much the stronger impression; for undulations will be thus excited in the fluid of the labyrinth from two different though contiguous points, and by the crossing of these undulations, stationary waves of increased intensity will be produced in the fluid. Müller's experiments shew that the same vibrations of the air act upon the fluid of the labyrinth with much greater intensity through the medium of the chain of auditory bones and the fenestra ovalis, than through the medium of the air of the tympanum and the membrane closing the fenestra rotunda: but the cases of disease in which the ossicula have been lost without loss of hearing, prove that sound may also be well conducted through the air of the tympanum and the membrane of the fenestra rotunda.

### *Functions of the Labyrinth.*

*The fluid of the labyrinth or perilymph* is the most general and constant of the acoustic provisions of the labyrinth. In all forms of organs of hearing, the sonorous vibrations affect the auditory nerve through the medium of a fluid: and the reason for this provision is probably to be found in the following circumstances. The ultimate purpose of the organ of hearing is to impart, as perfectly as possible, the impulses of the sonorous vibrations to the fibres of the auditory nerve.

This nerve being soft, and like all nerves, impregnated with water, sonorous undulations, if directly communicated to it from solid parts, would be partly converted into undulations of a fluid, before producing their impression on the fibres. Besides, however, the impregnation of the nervous fibres with water, on which their softness depends, all the interspaces between the fibres are, as in all soft tissues, filled with fluid matters, either blood or the fluid of cellular membrane. Hence the auditory nerve, in receiving the sonorous undulations through the medium of the fluid of the labyrinth, receives them from a medium of the same kind as that which occupies all the pores and interstices of the nervous fibres themselves. On this account, the vibration of the particles in the nerve itself will probably be much more uniform in character than if the surfaces of the nerve had been in contact with solid parts: in which case, the more internal particles of the nerve, being distant from the surface of the solid bone, would be acted on in a different manner from the more superficial particles.

The function usually ascribed to the *semicircular canals* is the collecting in their fluid contents, the sonorous undulations from the bones of the cranium. They have probably, also, in some degree the power of conducting sounds in the direction of their curved cavities more easily than the sounds are carried off by the surrounding hard parts in the original direction of the undulations, though this conducting power is in them much less perfect than in tubes containing air.

Admitting that they have these powers, the increased intensity of the sonorous vibrations thus attained will be of advantage in acting on the auditory nerve where it is expanded in the ampullæ of the canals, and in the utriculus. Where the membranous canals are in contact with the solid parietes of the tubes, this action must be much more intense. But the membranous semicircular canals must have a function independent of the surrounding hard parts; for in the Petromyzon

they are not separately enclosed in solid substance, but lie in one common cavity with the utriculus.

The *crystalline pulverulent masses* in the labyrinth would re-inforce the sonorous vibrations by their resonance, even if they did not actually touch the membranes upon which the nerves are expanded; but, inasmuch as these bodies lie in contact with the membranous parts of the labyrinth, and the vestibular nerve-fibres are imbedded in them, they communicate to these membranes and the nerves vibratory impulses of greater intensity than the fluid of the labyrinth can impart. This appears to be the office of the otoconia. Sonorous undulations in water are not perceived by the hand itself immersed in the water, but are felt distinctly through the medium of a rod held in the hand.

The *cochlea* seems to be constructed for the spreading out of the nervous fibres over a wide extent of surface, upon a solid lamina which communicates with the solid walls of the labyrinth and cranium, at the same time that it is in contact with the fluid of the labyrinth, and which, besides exposing the nervous fibres to the influence of sonorous undulations by two media, is itself insulated by fluid on either side.

The connection of the lamina spiralis with the solid walls of the labyrinth adapts the cochlea for the perception of the sonorous undulations propagated by the solid parts of the head and the walls of the labyrinth. The membranous labyrinth of the vestibule and semicircular canals is suspended free in the perilymph, and is destined more particularly for the perception of sounds through the medium of that fluid, whether the sonorous undulations be imparted to the fluid through the fenestræ, or by the intervention of the cranial bones, as when sounding bodies are brought into communication with the head or teeth. The spiral lamina on which the nervous fibres are expanded in the cochlea, is, on the contrary, continuous with the solid walls of the labyrinth, and receives directly from them the impulses which they transmit. This is an important advantage; for the impulses imparted by solid bodies have,

*cæteris paribus*, a greater absolute intensity than those communicated by water. And, even when a sound is excited in the water, the sonorous undulations are more intense in the water near the surface of the vessel containing it, than in other parts of the water equally distant from the point of origin of the sound: hence we may conclude that, *cæteris paribus*, the sonorous undulations of solid bodies act with greater intensity than those of water. Hence we perceive at once an important use of the cochlea.

This is not, however, the sole office of the cochlea; the spiral lamina, as well as the membranous labyrinth, receives sonorous impulses through the medium of the fluid of the labyrinth from the cavity of the vestibule, and from the fenestra rotunda. The lamina spiralis is, indeed, much better calculated to render the action of these undulations upon the auditory nerve efficient, than the membranous labyrinth is; for, as a solid body insulated by a different medium, it is capable of resonance.

Lastly, it may be observed, that the spreading out singly of the fibres of the nerve upon the lamina spiralis is advantageous, because, in the first place, it ensures a more complete participation of the fibres in the impulses communicated by the solid parts of the cochlea; and secondly, the intensity with which the sonorous undulations are communicated to a body, is proportionate to the extent of surface over which they can act on it.

### *Sensibility of the Auditory Nerve.*

Most frequently, several undulations or impulses on the auditory nerve concur in the production of the impressions of sound. But of the fact that a single impulse may be sufficient to excite the sensation, we have an example in the sound produced by an explosion, or the sudden division of air by the coming together of two previously separated bodies of air, as in crack-

ing a whip, etc. There is, at all events, nothing to refute this opinion; although it must be admitted that a single shock to the air will very readily excite a succession of undulations.

By the rapid succession of several impulses at unequal intervals, a noise or rattle is produced; from a rapid succession of several impulses at equal intervals, a musical sound results, the height or acuteness of which increases with the number of the impulses communicated to the ear within a given time. A sound of definite musical value is also produced when each one of the impulses, succeeding another thus at regular intervals, is itself compounded of several undulations, in such a way, that, heard alone, it would give the impression of an unmusical sound; that is to say, by a sufficiently rapid succession of short unmusical sounds at regular intervals, a musical sound is generated.

It would appear that two impulses, which are equivalent to four single or half vibrations, are sufficient to produce a definite note, audible as such through the auditory nerve. The note produced by the shocks of the teeth of a revolving wheel, at regular intervals upon a solid body, is still heard when the teeth of the wheel are removed in succession, until two only are left; the sound produced by the impulse of these two teeth, has still the same definite value in the scale of music.

The maximum and minimum of the intervals of successive impulses still appreciable through the auditory nerve as determinate sounds, have been determined by M. Savart. If their intensity is sufficiently great, sounds are still audible which result from the succession of 48,000 half vibrations, or 24,000 impulses in a second; and this, probably, is not the extreme limit in acuteness of sounds perceptible by the ear. For the opposite extreme, he has succeeded in rendering sounds audible which were produced by only fourteen or eighteen half vibrations, or seven or eight impulses, in a second; and sounds still deeper might probably be heard, if the individual impulses could be sufficiently prolonged.

By removing one or several teeth from the toothed wheel before mentioned, M. Savart was also enabled to satisfy himself of the fact that, in the case of the auditory nerve, as in that of the optic nerve, the sensation continues longer than the impression which causes it; for the removal of a tooth from the wheel produced no interruption of the sound. The gradual cessation of the sensation of sound renders it difficult, however, to determine its exact duration beyond that of the impression of the sonorous impulses.

The power of perceiving the *direction of sounds* is not a faculty of the sense of hearing itself, but is an act of the mind judging on experience previously acquired. From the modifications which the sensation of sound undergoes according to the direction in which the sound reaches us, the mind infers the position of the sounding body. The only true guide for this inference is the more intense action of the sound upon one than upon the other ear. But even here there is room for much deception, by the influence of reflexion or resonance, and by the propagation of sound from a distance, without loss of intensity through curved conducting-tubes filled with air. By means of such tubes, or of solid conductors, which convey the sonorous vibrations from their source to a distant resonant body, sounds may be made to appear to originate in a new situation.

The direction of sound may also be judged of by means of one ear only; the position of the ear and head being varied, so that the sonorous undulations at one moment fall upon the ear in a perpendicular direction, at another moment obliquely. But when neither of these circumstances can guide us in distinguishing the direction of sound, as when it falls equally upon both ears, its source being, for example, either directly in front or behind us, it becomes impossible to determine whence the sound comes.

Ventriloquists take advantage of the difficulty with which the direction of sounds is recognised, and also of the influence of the imagination over our judgment, when they direct their

voice in a certain direction, and at the same time pretend themselves to hear the sounds as coming from thence.

The *distance of the source of sounds* is not recognised by the sense itself, but is inferred from their intensity. The sound itself is always seated but in one place, namely in our ear; but it is interpreted as coming from an exterior soniferous body. When the intensity of the voice is modified in imitation of the effect of distance, it excites the idea of its originating at a distance; and this is also taken advantage of by ventriloquists.

The experiments of Savart, already referred to, prove that the effect of the action of sonorous undulations upon the nerve of hearing, endures somewhat longer than the period during which the undulations are passing through the ear. If, however, the impression of the same sound be very long continued, or constantly repeated for a long time, then the sensation produced may continue for a very long time, more than twelve or twenty-four hours even, after the original cause of the sound has ceased. This must have been experienced by every one who has travelled several days continuously; for some time after the journey the rattling noises are heard when the ear is not acted on by other sounds.

We have here a proof that the perception of sound as sound, is not essentially connected with the existence of undulatory pulses; and that the sensation of sound is a state of the auditory nerve, which, though it may be excited by a succession of impulses, may also be produced by other causes. The sensations of the retina remaining after the external impression of light has ceased, have been attributed to a retention of some of the matter of light for a certain time by the retina, as in the absorption of light by dark bodies; but in the case of the sense of hearing, such an hypothesis is evidently untenable. No irritating matter and no impulse can be here retained; and, even if it be supposed that undulations excited by the impulse are kept up in the auditory nerve for a certain time, they must be undulations of the nervous principle itself, which, being excited, continue until the equilibrium is restored.

Corresponding to the double vision of the same object with the two eyes, is the double hearing with the two ears; and analogous to the double vision with one eye, dependent on unequal refraction, is the double hearing of a single sound with one ear, owing to the sound coming to the ear through media of unequal conducting power. The first kind of double hearing is very rare; instances of it are recorded, however, by Sauvages and Itard. The second kind, which depends on the unequal conducting power of two media through which the same sound is transmitted to the ear, may easily be experienced. If a small bell be sounded in water, while the ears are closed by plugs, and a solid conductor is interposed between the water and the ear, two sounds will be heard differing in intensity and tone; one being conveyed to the ear through the medium of the atmosphere, the other through the conducting-rod.

The sense of vision may vary in its degree of perfection as regards either the faculty of adjustment to different distances, the power of distinguishing accurately the particles of the retina affected, sensibility to light and darkness, or the perception of the different shades of colour. In the sense of hearing there is no parallel to the faculty by which the eye is accommodated to distance, nor to the perception of the particular part of the nerve affected; but just as one person sees distinctly only in a bright light, and another only in a moderate light, so in different individuals the sense of hearing is more perfect for sounds of different pitch: and just as a person, whose vision for the forms of objects, etc., is acute, nevertheless distinguishes colours with difficulty, and has no perception of the harmony and disharmony of colours, so one, whose hearing is good as far as regards the sensibility to feeble sounds, is sometimes deficient in the power of recognising the musical relation of sounds, and in the sense of harmony and discord; while another individual, whose hearing is in other respects imperfect, has these endowments. The causes of these differences are unknown.

*Subjective sounds* are the result of a state of irritation or excitement of the auditory nerve produced by other causes than sonorous impulses. A state of excitement of this nerve, however induced, gives rise to the sensation of sound. Hence the ringing and buzzing in the ears heard by persons of irritable and exhausted nervous system, and by patients with cerebral disease, or disease of the auditory nerve itself; hence also the noise in the ears heard for some time after a long journey in a rattling noisy vehicle. Ritter found that electricity also excites a sound in the ears. From the above truly subjective sounds we must distinguish those dependent, not on a state of the auditory nerve itself merely, but on sonorous vibrations excited in the auditory apparatus. Such are the buzzing sounds attendant on vascular congestion of the head and ear, or on aneurismal dilatation of the vessels. Frequently, even the simple pulsatory circulation of the blood in the ear is heard. To the sounds of this class belong also the snapping sound in the ear produced by a voluntary effort, and the buzz or hum heard during the contraction of the palatine muscles in the act of yawning; during the forcing of air into the tympanum, so as to make tense the membrana tympani; and in the act of blowing the nose, as well as during the forcible depression of the lower jaw.

Irritation or excitement of the auditory nerve is capable of giving rise to movements in the body, and to sensations in other organs of sense. In both cases it is probable that the laws of nervous reflection, through the medium of the brain, come into play. An intense and sudden noise excites, in every person, closure of the eyelids, and in nervous individuals a start of the whole body, or an unpleasant sensation like that produced by an electric shock throughout the body, and sometimes a particular feeling in the external ear. Various sounds cause in many people a disagreeable feeling in the teeth, or a sensation of cold trickling through the body; and, in some people, intense sounds are said to make the saliva collect.

The sense of hearing may in its turn be affected by impressions on many other parts of the body; especially in diseases of the abdominal viscera, and in febrile affections. Here, also, it is probable that the central organs of the nervous system are the media through which the impression is transmitted.

### SENSE OF TASTE.

The conditions for the perception of taste are:—1, the presence of a nerve with special endowments; 2, the irritation of this nerve by the sapid matters; 3, the solution of these matters in the secretions of the organ of taste. The nerves concerned in the production of the sense of taste have been already considered (pp. 465-6).

The mode of action of the substances which excite taste probably consists in the production of a change in the internal condition of the gustatory nerves, and, according to the difference of the substances, an infinite variety of changes of condition, and consequently of tastes, may be induced. It is not, however, necessary for the manifestation of taste that sapid substances in solution should be brought into contact with its nerves. For the nerves of taste, like the nerves of other special senses, may have their peculiar properties excited by various other kinds of irritation, such as electricity and mechanical impressions. Thus Henle observed that a small current of air directed upon the tongue gives rise to a cool saline taste, like that of saltpetre; and Dr. Baly has shewn that a distinct sensation of taste, similar to that caused by electricity, may be produced by a smart tap applied to the papillæ of the tongue. Moreover, the mechanical irritation of the fauces and palate produces the sensation of nausea, which is probably only a modification of taste.

The matters to be tasted must either be in solution or be soluble in the moisture covering the tongue; hence insoluble

substances are usually tasteless, and produce merely sensations of touch. Moreover, for the perfect action of a sapid, as of an odorous substance, it is necessary that the sentient surface should be moist. Hence, when the tongue and fauces are dry, sapid substances, even in solution, are with difficulty tasted.

The principal, but not exclusive, seat of the sense of taste is the fauces and tongue. The tongue is a muscular organ whose use in relation to mastication and deglutition has already been considered (p. 204). The free surface is covered with structures analogous to those of the skin, namely, a *cutis* or *corium*, on which are placed *papillæ*, and which, together with them, is invested by *epithelium*.

The cutis is thinner and less dense than that of the skin, but is constructed of similar tissue, serves as a ground-work for the ramification of the abundant blood-vessels and nerves which the tongue receives, and affords insertion to the extremities of the muscular fibres of which the chief substance of the organ is composed.

The *papillæ* of the tongue are thickly set over its whole upper surface, giving to it its characteristic roughness. Their greater prominence than those of the skin is due to their interspaces not being filled up with epithelium, as the interspaces of the papillæ of the skin are. The papillæ of the tongue present several diversities of form; but three principal varieties, differing both in seat and general characters, may usually be distinguished. 1st. *Circumvallate* or *calyciform* papillæ, eight or ten in number, situate in two V-shaped lines at the base of the organ. These are circular elevations from $\frac{1}{20}$th to $\frac{1}{12}$th of an inch wide, each with a central depression, and surrounded by a circular fissure, at the outside of which again is a slightly-elevated ring; both the central elevation and the ring being formed of close-set simple papillæ. 2nd. *Fungiform* papillæ, scattered chiefly over the sides and tip, and sparingly over the middle of the dorsum, of the tongue; their name is derived from their being usually narrower at their base than their summit. These also consist of groups of

simple papillæ, each of which contains in its interior a loop of capillary blood-vessels, and a nerve-fibre. 3rd. Conical or *filiform* papillæ: these, which are the most abundant, are scattered over the whole surface, but especially over the middle of the dorsum. Their name denotes their shape.

The *epithelium* of the tongue is of the tesselated kind, like that of the epidermis (p. 318). It covers every part of the surface, but over the fungiform papillæ forms a thinner layer than elsewhere, so that these papillæ stand out more prominently than the rest. The epithelium covering the conical papillæ has been shewn by Todd and Bowman (xxxix. vol. i. p. 439), to have a singular arrangement; being extremely dense and thick, and projecting from their sides and summits in the form of long, stiff, hair-like processes. Many of these processes bear a close resemblance in structure to hairs, and some actually contain minute hair-tubes.

All the three varieties of papillæ just described have been commonly regarded as simple processes, like the papillæ of the skin; but Todd and Bowman have shewn that the surface of each kind is studded by minute conical processes of mucous membrane, which thus form secondary papillæ. These secondary papillæ also occur over most other parts of the tongue, not occupied by the compound papillæ. They are commonly buried beneath the epithelium; hence they have been hitherto overlooked.

Such, in outline, is the structure of the sensitive surface of the tongue. But the tongue is not the only seat of the sense of taste; for the results of experiments as well as ordinary experience shew that the soft palate and its arches, the uvula, tonsils, and probably the upper part of the pharynx, are endowed with taste. These parts, together with the base and posterior parts of the tongue, are supplied with branches of the glosso-pharyngeal nerve, and evidence has been already adduced (p. 465) that the sense of taste is conferred upon them by this nerve.

In most, though not in all, persons, the anterior part of the

tongue, especially the edges and tip, are supplied with taste. The middle of the dorsum is only feebly endowed with this sense, probably because of the density and thickness of the epithelium covering the filiform papillæ of this part of the tongue, which will prevent the sapid substances from penetrating to their sensitive parts. The use of these papillæ is, therefore, probably less for taste than for mechanical purposes in the act of mastication. The gustatory property of the anterior part of the tongue is due, as already said (pp. 456, 465), to the lingual branches of the fifth nerve.

Besides the sense of taste, the tongue, by means also of its papillæ, is endued, especially at its sides and tip, with a very delicate and accurate sense of touch, which renders it sensible of the impressions of heat and cold, pain and mechanical pressure, and consequently of the form of surfaces. The tongue may lose its common sensibility, and still retain the sense of taste, and *vice versâ*. This fact renders it probable that, although the senses of taste and of touch may be exercised by the same papillæ supplied by the same nerves, yet the nervous conductors for these two different sensations are distinct, just as the nerves for smell and common sensibility in the nostrils are distinct; and it is quite conceivable that the same nervous trunk may contain fibres differing essentially in their specific properties. Facts already detailed (p. 465) seem to prove that the lingual branch of the fifth nerve is the seat of sensations of taste in the anterior part of the tongue: and it is also certain, from the marked manifestations of pain to which its division in animals gives rise, that it is likewise a nerve of common sensibility. The glosso-pharyngeal also seems to contain fibres both of common sensation and of the special sense of taste.

The concurrence of common and special sensibility in the same part makes it sometimes difficult to determine whether the impression produced by a substance is perceived through ordinary sensitive fibres, or through those of the sense of taste.

In many cases, indeed, it is probable that both sets of nerve-fibres are concerned, as when irritating acrid substances are introduced into the mouth.

The impressions on the mind leading to the perception of taste seem to result, as already said, from certain changes in the internal condition of the nerves produced by the contact of sapid substances with the papillæ in which the fibres of these nerves are distributed. This explanation, obscure though it be, may account generally for the sense; but the variations of taste produced by different substances are as yet inexplicable. In the case of hearing, we know that sounds differ from one another according to the differences in the number of undulations producing them; and in the case of vision it is reasonably inferred that different colours result from differences in the number of undulations, or in the rate of transit, of the imponderable principle of light. But, in the cases of taste and smell, no such probable explanation has yet been offered. It would appear, indeed, from the experiments of Horn (clxxiii.), that while some substances taste alike in all regions of the tongue's surface, others excite different tastes, according as they are applied to different papillæ of the tongue. This observation, if confirmed, would seem to shew that, in some cases at least, different fibres are capable of receiving different impressions from the same sapid substance.

Much of the perfection of the sense of taste is often due to the sapid substances being also odorous, and exciting the simultaneous action of the sense of smell. This is shewn by the imperfection of the taste of such substances when their action on the olfactory nerves is prevented by closing the nostrils. Many fine wines lose much of their apparent excellence, if the nostrils are held close while they are drunk.

Very distinct sensations of taste are frequently left after the substances which excited them have ceased to act on the nerve; and such sensations often endure for a long time, and modify the taste of other substances applied to the tongue afterwards.

Thus, the taste of sweet substances spoils the flavour of wine, the taste of cheese improves it. There appears, therefore, to exist the same relation between tastes as between colours, of which those that are opposed or complementary render each other more vivid, though no general principles governing this relation have been discovered in the case of tastes. In the art of cooking, however, attention has at all times been paid to the consonance or harmony of flavours in their combination or order of succession, just as in painting and music the fundamental principles of harmony have been employed empirically while the theoretical laws were unknown.

Frequent and continued repetition of the same taste renders the perception of it less and less distinct, in the same way that a colour becomes more and more dull and indistinct, the longer the eye is fixed upon it. Thus, after frequently tasting first one and then the other of two kinds of wine, it becomes impossible to discriminate between them.

The simple contact of a sapid substance with the surface of the gustatory organ seldom gives rise to a distinct sensation of taste; it needs to be diffused over the surface and brought into intimate contact with the sensitive parts by compression, friction, and motion between the tongue and palate.

The sense of taste seems capable of being excited also by internal causes, such as changes in the conditions of the nerves or nervous centres produced by congestion or other causes, which excite subjective sensations in the other organs of sense. But little is known of the subjective sensations of taste; for it is difficult to distinguish the phenomena from the effects of external causes, such as changes in the nature of the secretions of the mouth.

## SENSE OF TOUCH.

The sense of touch is not confined to particular parts of the body of small extent, like the other senses; on the contrary, all parts capable of perceiving the presence of a stimulus by

ordinary sensation are, in various degrees, the seat of this sense; for touch is simply a modification or exaltation of common sensation or sensibility. The nerves on which the sense of touch depends are, therefore, the same as those which confer ordinary sensation on the different parts of the body, viz., the posterior ganglionic roots of the nerves of the spinal cord and the sensitive cerebral nerves.

But, although all parts of the body supplied with sensitive nerves are thus, in some degree, organs of touch, yet the sense is exercised in perfection only in those parts the sensibility of which is extremely delicate, *e. g.*, the skin, the tongue and the lips, which are provided with abundant papillæ.

The structure of the tongue and of its papillæ has been already considered. A general account has also been given of the structure of the skin and of its functions as an organ for excretion and absorption (p. 337); its peculiarities as a sensitive integument, and especially as an organ of touch, have now to be considered. By means of its toughness, flexibility, and elasticity, the skin is eminently qualified to serve as the general integument of the body, for defending the internal parts from external violence, and readily yielding and adapting itself to their various movements and changes of position. But, from the abundant supply of sensitive nerve-fibres which it receives, it is enabled to fulfil a not less important purpose in serving as the principal organ of the sense of touch. The entire surface of the skin is extremely sensitive, but its tactile properties are due, chiefly to the abundant papillæ with which it is studded. These papillæ have already been described as conical elevations of the corium, more prominent and more densely set at some parts than at others (p. 337). The parts on which they are most abundant and most prominent are the palmar surface of the hands and fingers, and the soles of the feet—parts, therefore, in which the sense of touch is most acute. Over other parts of the skin they are more or less thinly scattered, and are scarcely elevated above the surface. Their average length is about $\frac{1}{100}$th of an inch, and at their base they measure

about $\frac{1}{250}$th of an inch in diameter. Each papilla is abundantly supplied with blood, receiving from the vascular plexus in the cutis one or more minute arterial twigs, which divide into capillary loops in its substance, and then reunite into a minute vein, which passes out at its base. The abundant supply of blood which the papillæ thus receive explains the turgescence or kind of erection which they undergo when the circulation through the skin is active. The majority, but not all, of the papillæ contain also one or more terminal nerve-fibres, from the ultimate ramifications of the cutaneous plexus, on which their exquisite sensibility depends. The exact mode in which these nerve-fibres terminate is not yet satisfactorily determined. In some parts, especially those in which the sense of touch is highly developed, as, for example, the palm of the hand and the lips, the fibres appear to terminate, in many of the papillæ, by one or more free ends in the interior of a dilated oval-shaped body, not unlike a Pacinian corpuscle, occupying the principal part of the interior of the papilla, and termed, by Kölliker, an "axis-body." The nature of this body is obscure. Kölliker, Huxley, and others, regard it as little else than a mass of fibrous, or connective tissue, surrounded by elastic fibres, and formed, according to Huxley, by an increased development of the neurilemma of the nerve-fibres entering the papilla. Wagner, however, to whom seems to belong the merit of first describing these bodies, and who named them "corpuscula tactus," believes that, instead of thus consisting of a homogeneous mass of connective tissue, they are special and peculiar bodies of laminated structure, directly concerned in the sense of touch. They do not occur in all the papillæ of the parts where they are found, and, according to Wagner, those papillæ which possess them contain no blood-vessels, while, on the other hand, into the vascular papillæ no nerve-fibres enter. Kölliker and Huxley, however, have seen both blood-vessels and axis-bodies within the same papillæ; so that, although Wagner's statement on this point may be generally, yet it is not invariably, true. Since these peculiar bodies in

which the nerve-fibres end are only met with in the papillæ of highly sensitive parts, it may be inferred that they are specially concerned in the sense of touch, yet their absence from the papillæ of other tactile parts, shews that they are not essential to this sense.* In those instances in which the nerve-fibres do not thus terminate, they appear to form loops and to return.

Although destined especially for the sense of touch, the papillæ are not so placed as to come into direct contact with external objects; but, like the rest of the surface of the skin, are covered by one or more layers of epithelium, forming the cuticle or epidermis (p. 341). The papillæ adhere very intimately to the cuticle, which is thickest in the spaces between them, but tolerably level on its outer surface: hence, when stripped off from the cutis, as after maceration, its internal surface presents a series of pits and elevations corresponding to the papillæ and their interspaces, of which it thus forms a kind of mould. Besides affording by its impermeability a check to undue evaporation from the skin, and providing the sensitive cutis with a protecting investment, the cuticle is of service in relation to the sense of touch. For, by being thickest in the spaces between the papillæ, and only thinly spread over the summits of these processes, it may serve to subdivide the percipient surface of the skin into a number of isolated points, each of which is capable of receiving a distinct impression from an external body. By covering the papillæ it renders the sensation produced by external bodies more obtuse, and in this manner also is subservient to touch: for unless the very sensitive papillæ were thus defended, the contact of substances would give rise to pain, instead of the ordinary impressions of touch. This is shewn in the extreme sensitiveness and loss of tactile power in a part of the skin when deprived of its

* For the best account of these bodies, the nature of which, as already said, is still obscure, the student is referred to Wagner (lxxx. 1852, p. 493), Kölliker (ccvi. p. 86; ccxii. vol. ii.; and cxviii. 1860), Meissner (xiv. 1853, p. 342), and Huxley (ccxvii. vol. ii. p. 1.).

epidermis. If the cuticle is very thick, however, as on the heel, touch becomes imperfect, or is lost, through the inability of the tactile papillæ to receive impressions through the dense and horny layer covering them.

The sensations of the common sensitive nerves have as peculiar a character as those of any other organ of sense. The sense of touch renders us conscious of the presence of a stimulus, from the slightest to the most intense degree of its action, neither by sound, nor by light, nor by colour, but by that indescribable something which we call feeling, or common sensation. The modifications of this sense often depend on the extent of the parts affected. The sensation of pricking, for example, informs us that the sensitive particles are intensely affected in a small extent; the sensation of pressure indicates a slighter affection of the parts in a greater extent, and to a greater depth. It is by the depth to which the parts are affected, that the feeling of pressure is distinguished from that of mere contact. Schiff and Brown-Séquard (xxx. 1858) are of opinion that common sensibility and tactile sensibility manifest themselves to the individual by the aid of different sets of fibres. Dr. Sieveking has arrived at the same conclusion from pathological observation (cxc. 1858, vol. ii. p. 501).

By the sense of touch the mind is made acquainted with the size, form, and other external characters of bodies. And in order that these characters may be easily ascertained, the sense of touch is especially developed in those parts which can be readily moved over the surface of bodies. Touch, in its more limited sense, or the act of examining a body by the touch, consists merely in a voluntary employment of this sense combined with movement, and stands in the same relation to the sense of touch or common sensibility, generally, as the act of seeking, following, or examining odours, does to the sense of smell. Every sensitive part of the body which can, by means of movement, be brought into different relations of contact with external bodies, is an organ of "touch." No one part, consequently, has exclusively this function. The hand,

however, is best adapted for it, by reason of its peculiarities of structure,—namely, its capability of pronation and supination, which enables it, by the movement of rotation, to examine the whole circumference of a body; the power it possesses of opposing the thumb to the rest of the hand; and the relative mobility of the fingers.

In forming a conception of the figure and extent of a surface, the mind multiplies the size of the hand or fingers used in the inquiry by the number of times which it is contained in the surface traversed; and by repeating this process with regard to the different dimensions of a solid body, acquires a notion of its cubical extent.

The perfection of the sense of touch on different parts of the surface is proportioned to the power which such parts possess of distinguishing and isolating the sensations produced by two points placed close together. This power depends, at least in part, on the number of primitive nerve-fibres distributed to the part; for the fewer the primitive fibres which an organ receives, the more likely is it that several impressions on different contiguous points will act on only one nervous fibre, and hence be confounded, and perhaps produce but one sensation. Experiments to determine the tactile properties of different parts of the skin, as measured by this power of distinguishing distances, were made by E. H. Weber. One experiment consisted in touching the skin, while the eyes were closed, with the points of a pair of compasses sheathed with cork, and in ascertaining how close the points of the compasses might be brought to each other, and still be felt as two bodies. He examined, in this manner, nearly every part of the surface of the body, and has given tables shewing the relative degrees of sensibility of different parts. Experiments of a similar kind have been performed also by Valentin (iv. vol. ii. p. 566): and, among the numerous results obtained by both these investigators, it appears that the extremity of the third finger and the point of the tongue are the parts most sensitive: a distance of as little as half a line being here distinguished.

Next in sensitiveness to these is the mucous surface of the lips, which can perceive the two points of the compass when separated to the distance of about a line and a half: on the dorsum of the tongue they require to be separated two lines. The parts in which the sense of touch is least acute are the neck, the middle of the back, the middle of the arm, and the middle of the thigh, on which the points of the compass have to be separated to the distance of thirty lines to be perceived as distinct points (Weber). Other parts of the body possess various degrees of sensibility intermediate between the above extremes. (For Weber's table see xxxii. p. 752; for Valentin's, iv. vol. ii. p. 566.)

A sensation in a part endowed with touch appears to the mind to be, *cæteris paribus*, more intense when it is excited in a large extent of surface than when it is confined to a small space. The temperature of water into which he dipped his whole hand, appeared to Weber to be higher than that of water of really higher temperature, in which he immersed only one finger of the other hand. Similar observations may be made by persons bathing in warm or cold water.

Part of the ideas which we obtain of the conditions of external bodies is derived through the peculiar sensibility with which muscles are endowed—the sensibility by which we are made acquainted with their position, and the degree of their contraction. By this sensation, we are enabled to estimate the degree of force exerted in resisting pressure or in raising weights. The estimate of weight by muscular effort is more accurate than that by pressure on the skin, according to Weber, who states that by the former a difference between two weights may be detected when one is only one-twentieth or one-fifteenth less than the other. It is not the absolute, but the relative, amount of the difference of weight which we have thus the faculty of perceiving.

It is not, however, certain that our idea of the amount of muscular force used is derived solely from sensation in the muscles. We have the power of estimating very accurately

beforehand, and of regulating, the amount of nervous influence necessary for the production of a certain degree of movement. When we raise a vessel, with the contents of which we are not acquainted, the force we employ is determined by the idea we have conceived of its weight. If it should happen to contain some very heavy substance, as quicksilver, we shall probably let it fall; the amount of muscular action, or of nervous energy, which we had exerted, being insufficient. The same thing occurs sometimes to a person descending stairs in the dark; he makes the movement for the descent of a step which does not exist. It is possible that in the same way the idea of weight and pressure in raising bodies, or in resisting forces, may in part arise from a consciousness of the amount of nervous energy transmitted from the brain rather than from a sensation in the muscles themselves. The mental conviction of the inability longer to support a weight must also be distinguished from the actual sensation of fatigue in the muscles.

So, with regard to the ideas derived from sensations of touch combined with movements, it is doubtful how far the consciousness of the extent of muscular movement is obtained from sensations in the muscles themselves. The sensation of movement attending the motions of the hand is very slight; and persons who do not know that the action of particular muscles is necessary for the production of given movements do not suspect that the movement of the fingers, for example, depends on an action in the fore-arm. The mind has, nevertheless, a very definite knowledge of the changes of position produced by movements; and it is on this that the ideas which it conceives of the extension and form of a body are in great measure founded.

In order that an impression made on a sensitive surface may be perceived, it is necessary that there should exist a reciprocal influence between the mind and the sense of touch; for, if the mind does not thus co-operate, the organic conditions for the sensation may be fulfilled, but it remains unperceived. More-

over, the distinctness and intensity of a sensation in the nerves of touch depend, in great measure on the degree in which the mind co-operates for its perception. A painful sensation becomes more intolerable the more the attention is directed to it: thus, a sensation in itself inconsiderable, as an itching in a very small spot of the skin, may be rendered very troublesome and enduring.

As every sensation is attended with an idea, and leaves behind it an idea in the mind which can be reproduced at will, we are enabled to compare the idea of a past sensation with another sensation really present. Thus we can compare the weight of one body with another which we had previously felt of which the idea is retained in our mind. Weber was indeed, able to distinguish in this manner between temperatures, experienced one after the other, better than between temperatures to which the two hands were simultaneously subjected. This power of comparing present with past sensations diminishes, however, in proportion to the time which has elapsed between them.

The *after-sensations* left by impressions on nerves of common sensibility or touch are very vivid and durable. As long as the condition into which the stimulus has thrown the organ endures, the sensation also remains, though the exciting cause should have long ceased to act. Both painful and pleasurable sensations afford many examples of this fact.

The law of *contrast*, which we have shewn modifies the sensations of vision (p. 563), prevails here also. After the body has been exposed to a warm atmosphere, a degree of temperature a very little lower, which would under other circumstances appear warm, produces the sensation of cold ; and a sudden change to the extent of a few degrees from a cold temperature to one less severe, will produce the sensation of warmth. Heat and cold are, therefore, relative terms; for a particular state of the sentient organs causes what would otherwise be warmth to appear cold. So, also, a diminution in the intensity of a long-continued pain gives pleasure, even though the

degree of pain that remains would in the healthy state have seemed intolerable.

*Subjective sensations*, or sensations dependent on internal causes, are in no sense more frequent than in the sense of touch. All the sensations of pleasure and pain, of heat and cold, of lightness and weight, of fatigue, etc., may be produced by internal causes. Neuralgic pains, the sensation of rigor, formication or the creeping of ants, and the states of the sexual organs occurring during sleep, afford striking examples of subjective sensations.

The mind, also, has a remarkable power of exciting sensations in the nerves of common sensibility; just as the thought of the nauseous excites sometimes the sensation of nausea, so the idea of pain gives rise to the actual sensation of pain in a part predisposed to it. The thought of anything horrid excites the sensation of shuddering; the feelings of eager expectation, of pathetic emotion, of enthusiasm, excite in some persons a sensation of "concentration" at the top of the head, and of cold trickling through the body; fright causes sensations to be felt in many parts of the body; and even the thought of tickling excites that sensation in individuals very susceptible of it, when they are threatened with it by the movements of another person. These sensations from internal causes are most frequent in persons of excitable nervous systems, such as the hypochondriacal and the hysterical, of whom it is usual to say that their pains are imaginary. If by this is meant that their pains exist in their imagination merely, it is certainly quite incorrect. Pain is never imaginary in this sense; but is as truly pain when arising from internal as from external causes; the idea of pain only can be unattended with sensation, but of the mere idea no one will complain. Still, it is quite certain that the imagination can render pain that already exists more intense, and can excite it when there is a disposition to it.

# CHAPTER XIX.

## GENERATION AND DEVELOPMENT.

THE several organs and functions of the human body which have been considered in the previous chapters, have relation to the individual being. We have now to consider those organs and functions which are destined for the propagation of the species. These comprise the several provisions made for the formation, impregnation, and development of the ovum, from which the embryo or fœtus is produced and gradually perfected into a living human being.

The organs concerned in affecting these objects, are named the generative organs, or sexual apparatus, since part belong to the male and part to the female sex.

### *Generative Organs of the Female.*

The female organs of generation consist of two *Ovaries* for the formation of ova; of a *Fallopian tube*, or oviduct, connected with each ovary, for the purpose of conducting the mature ovum to the *uterus* or cavity in which, if impregnated, it is retained until the embryo is fully developed and fitted to maintain its existence, independent of internal connection with the parent; and, lastly, of a passage, or *vagina*, with its appendages, for the reception of the male generative organ in the act of copulation, and for the subsequent discharge of the fœtus.

The *ovaries* are two oval compressed bodies, situated in the cavity of the pelvis, one on each side, enclosed in the folds of the broad ligament. Each ovary is attached to the uterus by a narrow fibrous cord (the ligament of the ovary), and, more slightly, to the Fallopian tube by one of the fimbriæ into which the walls of the extremity of the tube expand. The

ovary is enveloped by a *capsule* of dense fibro-cellular tissue, which again is surrounded by peritoneum. The internal structure of the organ consists of a peculiar soft fibrous tissue, or *stroma*, abundantly supplied with blood-vessels, and having imbedded in it, in various stages of development, numerous minute follicles or vesicles, the *Graafian vesicles*, or sacculi containing the ova. A further account of the Graafian vesicles and of their contained ova will be presently given.

The *Fallopian tubes* are about four inches in length, and extend between the ovaries and the upper angles of the uterus. At the point of attachment to the uterus, the Fallopian tube is very narrow, but in its course to the ovary it increases to about a line and a half in thickness; at its distal extremity, which is free and floating, it bears a number of *fimbriæ*, one of which, longer than the rest, is attached to the ovary. The canal by which each Fallopian tube is traversed is narrow, especially at its point of entrance into the uterus, at which it will scarcely admit a bristle; its other extremity is wider, and opens into the cavity of the abdomen, surrounded by the zone of fimbriæ. Externally, the Fallopian tube is invested with peritoneum; internally, its canal is lined with mucous membrane, covered with ciliary epithelium (p. 490): between the peritoneal and mucous coats, the walls are composed, like those of the uterus, of fibrous tissue and organic muscular fibres.

The *uterus* is a somewhat pyriform, fibrous organ, with a central cavity lined with mucous membrane. In the unimpregnated state it is about three inches in length, two in breadth at its upper part, or *fundus*, but at its lower pointed part or *neck*, only about half an inch. The part between the fundus and neck is termed the body of the uterus: it is about an inch in thickness. The walls of the organ are composed of dense fibro-cellular tissue, with which are intermingled fibres of organic muscle: in the impregnated state the latter are much developed and increased. The cavity of the uterus corresponds in form to that of the organ itself: it is very small in the unimpregnated state; the sides of its mucous surface being

almost in contact, and probably only separated from each other by mucus. Into its upper part, at each side, opens the canal of the corresponding Fallopian tube: below, it communicates with the vagina by a fissure-like opening in its neck, the *os uteri*, the margins of which are distinguished into two lips, an anterior and posterior. At the mucous membrane of the cervix are found several mucous follicles, termed Ovula or glandulæ Nabothi: they probably form the jelly-like substance by which the os uteri is usually found closed.*

The *vagina* is a membranous canal, six or eight inches long, extending obliquely downwards and forwards from the neck of the uterus, which it embraces, to the external organs of generation. It is lined with mucous membrane; which in the ordinary contracted state of the canal, is thrown into transverse folds. External to the mucous membrane, the walls of the vagina are constructed of fibro-cellular tissue, within which, especially around the lower part of the tube, is a layer of erectile tissue. The anterior extremity of the vagina is embraced by an orbicular muscle, the constrictor vaginæ; its external orifice is, in the virgin, partially closed by a fold or ring of mucous membrane termed the *hymen*. The external organs of generation consist of the *clitoris*, a small elongated body, situated above and in the middle line, and constructed, like the male penis, of two erectile corpora cavernosa, and surmounted by an imperforate glans and prepuce: of two folds of mucous membrane, termed *labia interna*, or *nymphæ;* and in front of these, two other folds, the *labia externa*, or *pudenda*, formed of the external integument, and lined internally by mucous membrane. Between the nymphæ and beneath the clitoris is an angular space, termed the vestibule, at the centre of whose base is the orifice of the meatus urinarius. Numerous mucous follicles are scattered beneath the mucous membrane composing these parts of the external

* For an account of the arrangement of the fibres of the uterus, see xxxvii. Jan. 1845.

organs of generation; and at the side of the fore part of the vagina, are two larger lobulated glands, named *vulvo-vaginal*, or Duvernay's glands, which are analogous to Cowper's glands in the male.

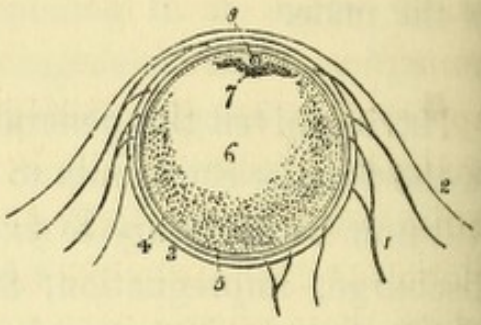
Having given this general outline of the several parts which, in the female, contribute to the reproduction of the species, it will now be necessary to examine successively the formation, discharge, impregnation, and development of the ovum, to which these several parts are subservient.

### *Unimpregnated Ovum.*

If the *structure and formation* of the human ovary be examined at any period between early infancy and advanced age, but especially during that period of life in which the power of conception exists, it will be found to contain, on an average, from fifteen to twenty small vesicles or membranous sacs of various sizes; these have been already alluded to as the *follicles* or *vesicles* of *De Graaf*, the anatomist who first accurately described them. At their first formation, the Graafian vesicles are small and deeply-seated in the substance of the ovary; but as they increase in size, they make their way towards the surface; and when mature, they form little prominences on the exterior of the ovary, covered only by the peritoneum. Each follicle is formed with an external membranous envelope, composed of fine fibro-cellular tissue, and connected with the surrounding stroma of the ovary by networks of blood-vessels (fig. 68). This envelope or tunic is lined with a layer of nucleated cells, forming a kind of epithelium or internal tunic and named *membrana granulosa*. The cavity of the follicle is filled with an albuminous fluid in which microscopic granules float; and it contains also the *ovum* or *ovule*. The ovum is a minute spherical body situated, in immature follicles, near

their centre; but in those nearer maturity, in contact with the membrana granulosa at that part of the follicle which forms a prominence on the surface of the ovary. The cells of the membrana granulosa are at that point more numerous than elsewhere, and are heaped around the ovum, forming a kind of granular zone, the *discus proligerus* (fig. 68).

*Fig.* 68.*




In order to examine an ovum, one of the Graafian vesicles, it matters not whether it be of small size or arrived at maturity, should be pricked, and the contained fluid received upon a piece of glass. The ovum then, being found in the midst of the fluid by means of a simple lens, may be further examined with higher microscopic powers. Owing to its globular form, however, its structure cannot be seen until it is subjected to gentle pressure.

The human ovum is extremely small, measuring, according to Bischoff, from $\frac{1}{240}$ to $\frac{1}{120}$ of an inch. Its external investment is a transparent membrane, about $\frac{1}{2500}$ of an inch in thickness, which, under the microscope, appears as a bright ring (fig. 69), bounded externally and internally by a dark outline: it is called the *zona pellucida*, or *vitelline membrane*, and corresponds with the *chorion* of the impregnated ovum. It adheres externally to the heap of cells constituting the discus proligerus.

Within this transparent investment or zona pellucida, and

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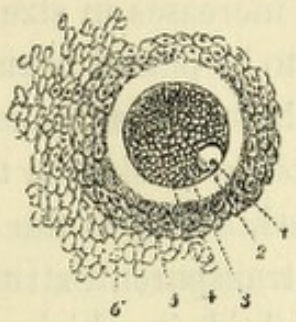
* Fig. 68. Section of the Graafian vesicle of a Mammal, after Von Baer. 1. Stroma of the ovary with blood-vessels. 2. Peritoneum. 3 and 4. Layers of the external coat of the Graafian vesicle. 5. Membrana granulosa. 6. Fluid of the Graafian vesicle. 7. Granular zone or discus proligerus, containing the ovum (8).

usually in close contact with it, lies the *yelk* or *vitellus*, which is composed of granules and globules of various sizes, imbedded in a more or less fluid substance. The smaller granules, which are the more numerous, resemble in their appearance, as well as their constant motion, pigment granules. The larger granules or globules which have the aspect of fat globules, are in greatest number at the periphery of the yelk. The number of the granules is, according to Bischoff, greatest in the ova of carnivorous animals. In the human ovum their quantity is comparatively small.

*Fig.* 69.*



The substance that combines the globules and granules of the yelk is, in many animals, quite fluid. The yelk then completely fills the cavity of the zona pellucida, and escapes in a liquid form when that membrane is ruptured: but in ova of the human subject and some animals the yelk is much more consistent, and sometimes escapes as a solid globular mass when the zona pellucida is torn. It is, according to Bischoff, solely owing to this firm consistence of the yelk that it, in many cases, preserves its form when a watery fluid passes by imbibition through the zona pellucida, and that an interval is then apparent between the yelk and that membrane. From the appearances resulting from the action of water on the ovum, and from other circumstances, it has been thought that the mass composing the yelk is surrounded by another membrane within the zona pellucida, but the evidence for such a view is not satisfactory (see clxxiv. p. 34.)

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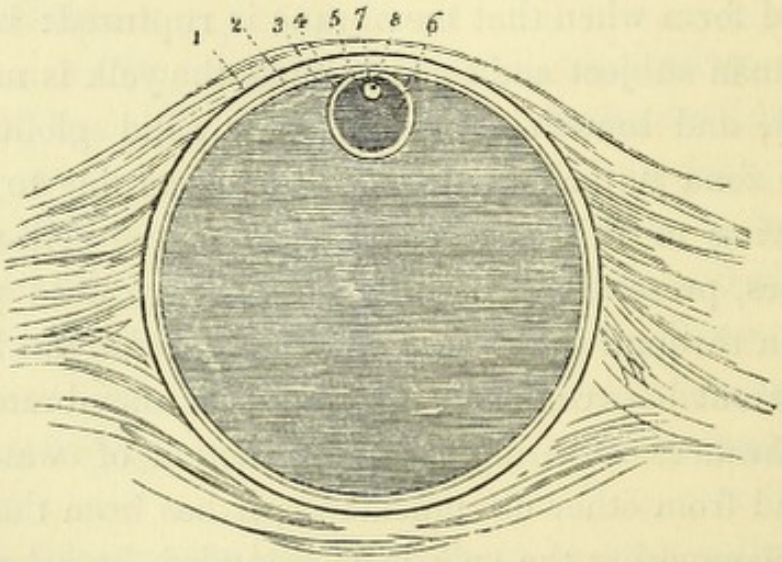
* Fig. 69. Ovum of the sow, after Barry. 1. Germinal spot. 2. Germinal vesicle. 3. Yelk. 4. Zona pellucida. 5. Discus proligerus. 6. Adherent granules or cells.

In the substance of the yelk is imbedded the *germinal vesicle*, or vesicula germinativa (figs. 69, 70). This vesicle is of greatest relative size in the smallest ova, and is in them surrounded closely by the yelk, nearly in the centre of which it lies. During the development of the ovum, the germinal vesicle increases in size much less rapidly than the yelk, and comes to be placed near to its surface. In a mature ovum of the rabbit it is about one-sixtieth of a line in diameter (Bischoff); its size in the human ovum has not yet been ascertained, owing to the difficulty of isolating it. It consists of a fine, transparent, structureless membrane, containing a clear watery fluid, in which are sometimes a few granules.

At that part of the periphery of the germinal vesicle which is nearest to the periphery of the yelk is situated the *germinal spot*, a finely granulated substance, of a yellowish colour,

*Fig.* 70.*




* Fig. 70. Diagram of a Graafian vesicle, containing an ovum. 1. Stroma or tissue of the ovary. 2 and 3. External and internal tunics of the Graafian vesicle. 4. Cavity of the vesicle. 5. Thick tunic of the ovum or yelk-sac. 6. The yelk. 7. The germinal vesicle. 8. The germinal spot.

strongly refracting the rays of light, and measuring, in the Mammalia generally, from $\frac{1}{3600}$ to $\frac{1}{2400}$ of an inch (Wagner).

Such are the parts of which the Graafian follicle and its contents, including the ovum, are composed. The diagram (fig. 70) represents them in their relative positions when mature.

It remains still to say something of the mode of development of, and subsequent changes in, these several parts especially in relation to the questions whether the Graafian vesicle is the immediate formative organ of the ovum; in what order the several parts of the ovum are formed; and the changes which they undergo in the progress of the ovum to maturity.

The first question may be answered in the affirmative, for the researches of Valentin and Bischoff have shewn, that the Graafian vesicle is formed previous to the ovum, which is subsequently developed in it. Bischoff and Barry agree, that the development of the Graafian vesicles and ova continues uninterruptedly from birth to the end of the fruitful period of woman's life. In some animals, as the cow and sow, it commences in the embryo, even at an early period of uterine existence, but in the dog and rabbit not till after birth. Bischoff describes the process of formation of the Graafian vesicles and ova to be as follows:—At first nothing can be distinguished in the substance of the ovary but primary cells and nuclei of cells; then round groups of similar cells are seen scattered in large numbers through the stroma. The peripheral cells of each of these groups subsequently coalesce, so as to form a homogeneous transparent vesicular membrane, while the portion of the mass within becomes fluid. Thus is formed the Graafian vesicle. On the inner wall of this follicle or vesicle new cells are formed in the manner of an epithelial layer, while the cavity is found to contain a transparent fluid with nuclei of cells and granules, exactly resembling yelk-granules suspended in it. The next stage is marked by the appearance of a second smaller transparent vesicle within the Graafian

vesicle. This second vesicle, which is the germinal vesicle, has a nucleus, the germinal spot. Granules, similar to yelk-granules, soon accumulate around the germinal vesicle; but the further steps in the development of the ovum could not be traced. All its parts were completely formed when Bischoff next observed it. A somewhat different account is given by Valentin (lxxx. 1838) of the mode in which the Graafian vesicle is developed, but he agrees with Bischoff that it is formed previous to the ovum.

With regard to the parts of the ovum first formed, it appears certain that the formation of the germinal vesicle precedes that of the yelk and zona pellucida, or vitelline membrane. Whether the germinal spot is formed first, and the germinal vesicle afterwards developed around it, cannot be decided in the case of vertebrate animals; but the observations of Kölliker and Bagge on the development of the ova of intestinal worms shew that in these animals, the first step in the process is the production of round bodies resembling the germinal spots of ova, the germinal vesicles being subsequently developed around these in the form of transparent membranous cells.

The more important changes that take place in the ovum subsequent to the formation of these, its essential component parts, consists in alterations of the size and position of these parts with relation to each other, and of the ovum itself with relation to the Graafian vesicle, and in the more complete elaboration of the yelk. The earlier the stage of development the larger is the germinal vesicle in relation to the whole ovum, and the ovum in relation to the Graafian vesicle. For, as the ovum becomes mature, although all these parts increase in size, the Graafian vesicle enlarges most, and the germinal vesicle least. Changes take place also in the position of the parts. The ovum at first occupies the centre of the Graafian vesicle, but subsequently is removed to its periphery. The germinal vesicle, too, which in young ova is in the centre of the yelk, is in mature ova found at the periphery.

The change of position of the ovum from the centre to the periphery of the Graafian vesicle is possibly connected with the formation of the membrana granulosa which lines the vesicle. For, according to Valentin (lxxx. 1838), at a very early period the contents of the vesicle between its wall and the ovum are almost wholly formed of granules; but in the process of growth a clear fluid collects in the centre of the vesicle, and the granules which from the first have a regular arrangement are pushed outwards, and form the membrana granulosa. Now as the mature ovum lies embedded in a thickened portion of the membrana granulosa, it is possible that when the elementary parts of this membrane are pushed outwards, in the way just described, the ovum is carried with them from the centre to the periphery of the follicle. While the changes here described take place, the zona pellucida increases in thickness.

According to Bischoff, the number of the granules of the yelk is greater the more mature the ovum, consequently the yelk is more opaque in the mature, and more transparent in the immature ova. The matter in which the granules are contained is fluid in the immature ova of all animals; in some it remains so; but in others, as the human ovum, it subsequently becomes a consistent gelatinous substance.

From the earliest infancy, and through the whole fruitful period of life, there appears to be a constant formation, development, and maturation of Graafian vesicles, with their contained ova. Until the period of puberty, however, the process is comparatively inactive; for, previous to this period, the ovaries are small and pale, the Graafian vesicles in them are very minute, few in number, and probably never attain full development, but soon shrivel and disappear instead of bursting as matured follicles do; the contained ova are also incapable of being impregnated. But, coincident with the other changes which occur in the body at the time of puberty, the ovaries enlarge, and become very vascular, the formation of Graafian vesicles is more abundant, the size and degree of

development attained by them are greater, and the ova are capable of being fecundated.

### *Discharge of the Ovum.*

In the process of development of individual vesicles, it has been already observed, that as each increases in size it gradually approaches the surface of the ovary, and when fully ripe or mature, forms a little projection on the exterior. Coincident with the increase of size caused by the augmentation of its liquid contents, the external envelope of the distended vesicle becomes very thin and eventually bursts. By this means the ovum and fluid contents of the Graafian vesicle are liberated, and escape on the exterior of the ovary, whence they pass into the Fallopian tube, the fimbriated processes of the extremity of which are supposed coincidently to grasp the ovary, while the aperture of the tube is applied to the part corresponding to the matured and bursting vesicle.

In animals whose capability of being impregnated occurs at regular periods, as in the human subject, and most Mammalia, the Graafian vesicles and their contained ova appear to arrive at maturity, and the latter to be discharged, at such periods only. But in other animals, *e.g.*, the common fowl, the formation, maturation, and discharge of ova appear to take place almost constantly.

It has long been known, that in the so-called oviparous animals the separation of ova from the ovary may take place independently of impregnation by the male, or even of sexual union. And it is now established, especially by the labours of Bischoff (clxxvii.), Raciborski (clxxviii), and Pouchet (clxxix), that a like maturation and discharge of ova, independently of coition, occurs in Mammalia, and most probably also in the human subject: the periods at which the matured ova are separated from the ovaries and received into the Fallopian tubes being indicated, in Mammalia, by the

phenomena of *heat* or *rut*; in the human female, by the phenomena of *menstruation*. Sexual desire manifests itself in the human female with greater intensity at these periods, and in the female of mammiferous animals at no other time. If the union of the sexes takes place, the ovum may be fecundated, but if no union occurs it perishes.

In proof that the phenomena of heat in mammiferous animals are coincident with the discharge of ova from the ovaries, independent of the influence of the male, abundant evidence has been collected. Thus Blundell (xli. vol. x.), Hausmann (clxxv.), and Bischoff (clxxvii.), observed that, when one oviduct or one half of the uterus had been tied or divided in an animal previous to coitus, although fœtuses are subsequently met with only on that side on which the passage to and from the ovary remains free, yet ruptured ovarian vesicles, or corpora lutea, are found in *both* ovaries. And Dr. Blundell has shewn that the result, as regards the ovaries, is the same as if the vagina be divided near the mouth of the uterus, so as to completely to interrupt its canal, and to prevent the seminal fluid from reaching even the uterus; although, of course, no embryoes are produced in this case. These experiments proved that Graafian vesicles burst independently of the contact of the seminal fluid; but still they left room for the objection that the rupture of the vesicles might have been caused by the excitement attending sexual connection. This objection, however, is removed by the fact observed by many physiologists, that if mammiferous animals, which have been kept separate from the male, be killed during the period of heat, the Graafian follicles will be found either turgid and extremely vascular, or already burst: and still more completely by the investigations of Bischoff and Raciborski, who have demonstrated the discharge of ova in the ovaries, although no sexual union had taken place. Thus, to mention one among several conclusive observations, Bischoff, having remarked that a large bitch in his possession commenced to be in heat on the 18th and 19th of December, kept her closely shut up, and on the 23rd (having

previously, on the 21st, ascertained that she was disposed to receive the male, though he did not permit coitus to take place), he cut out the left ovary and Fallopian tube, and closed the wound by suture. On examining the ovary, he found that no Graafian follicles had yet opened, though four of them were much swollen, undergoing the changes preparatory to the discharge of the ova. Five days later he killed the animal, and found that rupture of the follicles in the remaining right ovary had taken place: and on examining the Fallopian tube, he found the four extruded ova close together, at a distance of about three inches down the tube.

It is certain, then, that in mammiferous animals, as in the lower classes, ova are brought to maturity and discharged from the ovaries independently of sexual union. That this maturation and discharge occur periodically, and only during the phenomena of heat, is made probable by the facts that, in all the instances in which Graafian vesicles have been found presenting the appearance of recent rupture, the animals were at the time, or had recently been, in heat; that, on the other hand, there is no authentic and detailed account of Graafian vesicles being found ruptured in the intervals of the periods of heat; and that female animals do not admit the males, and never become impregnated, except at those periods.

Many circumstances make it probable that the human female is subject, in these respects, to the same law as the females of other mammiferous animals; namely, that in her as in them, ova are matured and discharged from the ovary independent of sexual union, and that this maturation and discharge occur periodically at the epochs of menstruation. Thus Graafian vesicles recently ruptured have been frequently seen in ovaries of virgins or women who could not have been recently impregnated, and although it is true that the ova discharged under these circumstances have rarely been discovered in the Fallopian tube,* partly on account of their

* See, however, the record of two such cases by Dr. Letheby, in the Philosophical Transactions 1851.

minute size, and partly because the search has seldom been prosecuted with much care; yet analogy forbids us to doubt that in the human female, as in the domestic quadrupeds, the result and purpose of the rupture of the follicles is the discharge of the ova.

The evidence of the periodical discharge of ova at the epochs of menstruation is first, that nearly all authors who have touched on the point, agree that no traces of follicles having burst, are ever seen in the ovaries before puberty or the first menstruation; secondly, that in all cases in which ovarian follicles have been found burst independently of sexual intercourse, the women were at the time menstruating, or had very recently passed through the menstrual state; thirdly, that although in women sexual connection is not confined to the periods of menstruation, yet conception is more likely to occur within a few days after the cessation of the menstrual flux than at other times; and, lastly, that the ovaries of the human female become turgid and vascular at the menstrual periods, as those of animals do at the time of heat.

From what has been said, it may, therefore, be concluded that the two states, heat and menstruation, are analogous, and that the essential accompaniment of both is the maturation and extrusion of ova. In both there is a state of active congestion of the sexual organs, sympathising with the ovaries at the time of the highest degree of development of the Graafian vesicles; and in both the crisis of this state of congestion is attended by a discharge of blood or mucus, or both, from external organs of generation.

The occurrence of a menstrual discharge is one of the most prominent indications of the commencement of puberty in the female sex; though its absence even for several years is not necessarily attended with arrest of the other characters of this period of life, or with inaptness for sexual union or incapability of impregnation. The average time of its first appearance in females of this country and others of about the same latitude, is from fourteen to fifteen; but it is much influenced

by the kind of life to which girls are subject, being accelerated by habits of luxury and indolence, and retarded by contrary conditions. On the whole, its appearance is earlier in persons dwelling in warm climes than in those inhabiting colder latitudes; though the extensive investigations of Mr. Robertson shew that the influence of temperature on the development of puberty has been exaggerated. Much of the influence attributed to climate appears due to the custom prevalent in many hot countries, as in Hindostan, of giving girls in marriage at a very early age, and inducing sexual excitement previous to the proper menstrual time. The menstrual functions continue through the whole fruitful period of a woman's life, and usually cease between the forty-fifth and fiftieth years.

The several menstrual periods occur usually at intervals of a lunar month, the duration of each being from three to six days. In some women the intervals are as short as three weeks, or even less; while in others they are longer than a month. The periodical return is usually attended by pain in the loins, a sense of fatigue in the lower limbs, and other symptoms which are different in different individuals. Menstruation does not usually occur in pregnant women, or in those who are suckling; but instances of its occurrence in both these conditions are by no means rare.

The menstrual discharge consists of blood effused from the inner surface of the uterus, and mixed with mucus from the uterus, vagina, and external parts of the generative apparatus. Being diluted by this admixture, the menstrual blood coagulates less perfectly than ordinary blood; and the frequent acidity of the vaginal mucus tends still further to diminish its coagulability. This has led to the supposition that the menstrual blood contains an unusually small quantity of fibrine, or none at all. The blood-corpuscles exist in it in their natural state: mixed with them also may be found numerous scales of epithelium derived from the mucous passages along which the discharge flows.*

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* For all relating to the periods of commencement and cessation of

Immediately before, as well as subsequent to, the rupture of a Graafian vesicle and the escape of its ovum, certain changes ensue in the interior of the vesicle, which result in the production of a yellowish mass termed a *corpus luteum*.

When fully formed, the corpus luteum of mammiferous animals is a roundish solid body, of a yellow or orange colour, and composed of a number of lobules which surround, sometimes a small cavity, but more frequently a small stelliform mass of white substance, from which delicate processes pass as septa between the several lobules. Very often, in the cow and sheep, there is no white substance in the centre of the corpus luteum; and the lobules projecting from the opposite walls of the Graafian vesicle appear in a section to be separated by the thinnest possible lamina of semi-transparent tissue.

When a Graafian vesicle is about to burst and expel the ovum, it becomes highly vascular and opaque; and, immediately before the rupture takes place, its walls appear thickened on their interior by a reddish glutinous or fleshy-looking substance. Immediately after the rupture, the inner layer of the wall of the vesicle appears pulpy and flocculent. It is thrown into wrinkles by the contraction of the outer layer, and, soon, red fleshy mammillary processes grow from it, and gradually enlarge till they nearly fill the vesicle, and even protrude from the orifice in the external covering of the ovary. Subsequently this orifice closes, but the fleshy growth within still increases during the earlier period of pregnancy, the colour of the substance gradually changing from red to yellow, and its consistence becoming firmer.

The corpus luteum of the human female (fig. 71) differs from that of the domestic quadruped in being of a firmer texture, and having more frequently a persistent cavity at its centre,

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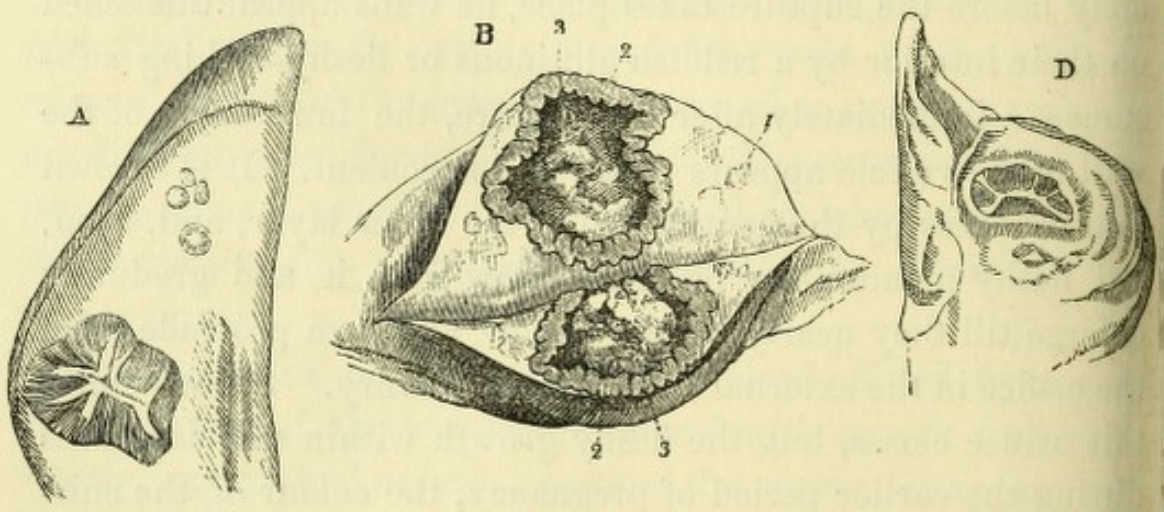
the menstrual functions, and the conditions by which they are delayed or accelerated, consult especially Raciborski (clxxvii.); Pouchet (clxxix.); Dr. Guy (lxxxviii. 1845); and Mr. Roberton in several of the volumes of the Edinburgh Medical and Surgical Journal.

and in the stelliform cicatrix, which remains in the cases where the cavity is obliterated, being proportionately of much larger bulk. The quantity of yellow substance formed is also much less: and, although the deposit increases after the vesicle has burst, yet it does not usually form mammillary growths projecting into the cavity of the vesicle, and never protrudes from the orifice, as is the case in other Mammalia. It maintains the character of a uniform, or nearly uniform layer, which is thrown into wrinkles in consequence of the contraction of the external tunic of the vesicle. After the orifice of the vesicle has closed, the growth of the yellow substance continues during the first half of pregnancy, till the cavity is reduced to a comparatively small size, or is obliterated; in the latter case, merely a white stelliform cicatrix remains in the centre of the corpus luteum.

*Fig.* 71.*




An effusion of blood generally takes place into the cavity of the Graafian vesicle at the time of its rupture, especially in the

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* Fig. 71. Corpora lutea of different periods. B. Corpus luteum of about the sixth week after impregnation, showing its plicated form at that period. 1. Substance of the ovary. 2. Substance of the corpus luteum. 3. A greyish coagulum in its cavity; after Dr. Paterson. A. Corpus luteum, two days after delivery. D. In the twelfth week after delivery. After Dr. Montgomery.

human subject; but it has no share in forming the yellow body; it gradually loses its colouring matter, and acquires the character of a mass of fibrine. The serum of the blood sometimes remains included within a cavity in the centre of the coagulum, and then the decolorized fibrine forms a membraniform sac, lining the corpus luteum. At other times the serum is removed, and the fibrine constitutes a solid stelliform mass.

The yellow substance of which the corpus luteum consists, both in the human subject and in the domestic animals, is a growth from the inner surface of the Graafian vesicle, the result of an increased development of the cells forming the membrana granulosa which naturally lines the internal tunic of the vesicle.

The first changes of the internal coat of the Graafian vesicle in the process of formation of a corpus luteum, seem to occur in every case in which an ovum escapes; as well as in the human subject as in the domestic quadrupeds. If the ovum is impregnated, the growth of the yellow substance goes on during nearly the whole period of gestation, and forms the large corpus luteum commonly described as a characteristic mark of impregnation. If the ovum is not impregnated, the growth of yellow substance on the internal surface of the vesicle proceeds, in the human ovary, no further than the formation of a thin layer, which shortly disappears; but in the domestic animals it continues for some time after the ovum has perished, and forms a corpus luteum of considerable size. The fact that a structure, in its essential characters similar to, though smaller than, a corpus luteum, observed during pregnancy, is formed in the human subject independent of impregnation or of sexual union, coupled with the varieties in size of corpora lutea formed during pregnancy, necessarily renders unsafe all evidence of previous impregnation founded on the existence of a corpus luteum in the ovary.*

* For a full discussion of all the facts relating to this question see Dr. Baly, in the Supplement to the second edition of Müller's Physiology.

## IMPREGNATION OF THE OVUM.

### *Male Sexual Functions.*

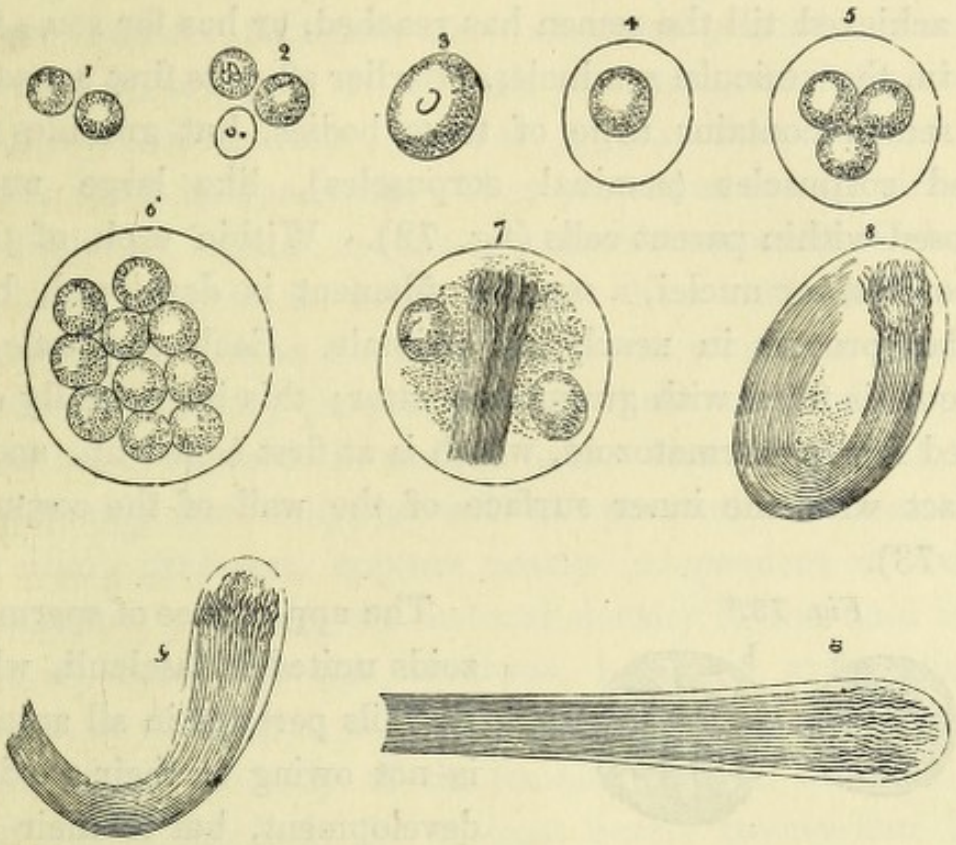
The fluid of the male, by which the ovum is impregnated, consists essentially of the semen secreted by the testicles; and, to this are added, as necessary, perhaps, to its perfection, a material secreted by the vesiculæ seminales, in which, as in reservoirs, the semen lies before its discharge, and the secretion of the prostate gland, and of Cowper's glands. Portions of these several fluids are, probably, all discharged together with the proper secretion of the testicles.

The secreting structure of the testicle is disposed in two contiguous parts—the body of the testicle, and the epididymis, enclosed within a tough fibrous membrane, the *tunica albuginea*. The vas deferens, the main trunk of the secreting tube passing to the lower part of the epididymis, assumes there a much less diameter, with a very tortuous course: with its various convolutions it forms first the mass named *caput minor*, then the *body*, and then the *caput major* of the epididymis. At the last-named part, the duct divides into ten or twelve small branches, the convolutions of which form coniform masses named *coni vasculosi*; and the vessels continued from these, after anastomoses in what is called the *rete testis*, lead finally to the tubules which form the proper substance of the testicle, wherein they are arranged in lobules, closely packed, and all attached to the tough fibrous tissue at the back of the testicle.

The tubes, *seminal tubes*, or *tubuli seminiferi*, which compose the proper substance of the testicle, are fine thread-like tubules, formed of simple homogeneous membrane, measuring on an average $\frac{1}{100}$th to $\frac{1}{200}$th of an inch, and lined with epithelium or gland-cells. They rarely branch, extend as simple tubes through a great length, with the same uniform structure, and probably terminate in loops. Their walls are

covered with fine capillary blood-vessels, through which, reckoning their great extent in comparison with the size of the spermatic artery, the blood must move very slowly.

*Fig.* 72.*



The *seminal fluid* secreted by the testicle is one of those secretions in which a process of development is continued after

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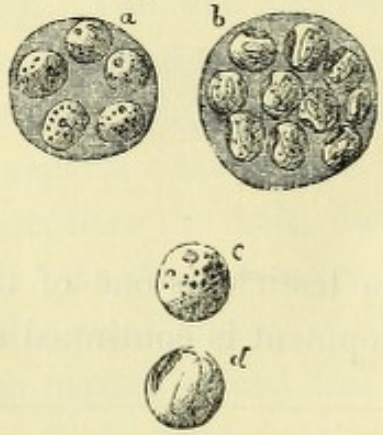
* Fig. 72. Development of the spermatozoids of Certhia familiaris (the common Creeper); after Wagner. 1. Granules of the semen, granula seminis, obtained from the testicle when very much reduced in size during the winter; 2 to 10, different bodies found in the semen, taken from the testicle when very turgid during the summer; 2, 3, granula seminis of which many are probably merely cells of epithelium; 4, 5, 6. cysts, or parent cells, containing one or several round granular globules or nuclei. 7, a similar cyst, in which are two globules, together with a mass of granules, and a fasciculus of spermatozoids in the process of development; 8, a similar cyst, become oval in form, while the spermatozoids have enlarged and are curled up within it; 9, 10, cysts and fasciculi of spermatozoids still further developed; in 10, the fasciculus is ready to divide into separate filaments.

its formation by the secreting cells, and its discharge from them into the tubes. The principal part of this development consists in the formation of the peculiar bodies named *seminal filaments*, *spermatozoa*, or *spermatozoids* (fig. 72), the complete development of which, in their full proportion of number, is not achieved till the semen has reached, or has for some time lain in, the vesiculæ seminales. Earlier after its first secretion, the semen contains none of these bodies, but granules and round corpuscles (seminal corpuscles), like large nuclei, enclosed within parent cells (fig. 72). Within each of these corpuscles, or nuclei, a seminal filament is developed, by a similar process in nearly all animals, Each corpuscle, or nucleus, is filled with granular matter; this is gradually converted into a spermatozoid, which is at first coiled up, and in contact with the inner surface of the wall of the corpuscle (fig. 73).

*Fig.* 73.*




The appearance of spermatozoids united in fasciculi, which prevails perhaps in all animals, is not owing to their mode of development, but to their tendency, when set free from their formative cellules or nuclei, to arrange themselves thus: a tendency showing that their bodies attract each other in the same way that blood-disks do in the formation of *rouleaux*. The fasciculi are formed within the parent cell when this remains entire after the nuclei or cellules are dissolved; in other cases they are formed in the seminal fluid by the union of spermato-

* Fig. 73. It represents the development of the spermatozoids of the rabbit. *a*. A parent cell or cyst, with five cellules or nuclei. *b*. A parent cell with ten cellules, each of which contains a spermatic filament. *c*. A free cellule or nucleus, with a nucleolus and granules, more highly magnified. *d*. A cellule in which a spermatic filament is seen, the granules having disappeared.

zoids which have been wholly set free by the solution of both parent-cell and nuclei.

Thus developed, the human seminal filaments consist of a long, slender, tapering portion, called the body or tail, to distinguish it from the head, an oval or pyriform portion of larger diameter, flattened, and sometimes pointed. They are from $\frac{1}{500}$th to $\frac{1}{600}$th of an inch in length, the length of the head alone being from $\frac{1}{5000}$th to $\frac{1}{3000}$th of an inch, and its width about half as much. They present no trace of structure, or dissimilar organs; a dark spot often observed in the head is, probably, due to its being concave like a blood corpuscle. They move about in the fluid like so many minute corpuscles, with each a ciliary process, lashing their tails, and propelling their heads forwards in various lines. Their movement, which is probably essentially, as well as apparently, similar to that of ciliary processes, appears nearly independent of external conditions, provided the natural density of the fluid is preserved; disturbing this condition, by either evaporating the semen, or diluting it, will stop the movement. It may continue within the body of the female for seven or eight days, and out of the body for at least nearly twenty-four hours. The direction of the movement is quite uncertain: but, in general, the current that each excites keeps it from the contact of others. The rate of motion, according to Valentin, is about one inch in thirteen minutes.

Respecting the purpose served by these seminal filaments, little that is certain can be said. Their occurrence in the impregnating fluid of nearly all classes of animals, proves their essentiality to the process of impregnation. They have been sometimes regarded as highly organized, and as, in some sense or other, the materials or organs out of which the new individual is begun; by others they are considered as a kind of parasitic animalcules. But, probably, all such theories of them are erroneous. Their want of structure, and their development in cells, not by generation or succession, are inconsistent with the notion of their being in any sense, distinct animals;

neither is there evidence for believing that their entire substance is employed in the construction of the embryo. It is not safe to assume more than that they, like the blood-corpuscles, and the corpuscles of other secretions, elaborate the fluid in which they are placed, while themselves are being developed and growing; that they may therefore be regarded as a kind of floating gland-corpuscles. And, probably, they add to this function, that of assisting in the conveyance of the seminal fluid to the ovum; for they have been found, some time after the copulation of dogs and rabbits, covering the surface of the ovum in even the furthest part of the Fallopian tube; and wherever they are, they must carry with them some of the other constituents of the seminal fluid. So that they may be regarded as conveyers, as well as elaborators, of the seminal fluid. Whether their contact with the ovum be essential to its impregnation, is not quite determined; it probably is so, for the researches of Newport, Barry, Bischoff, and others, seemed to have proved, that in the process of fertilization, the spermatozoa penetrate bodily into the interior of the ova.

The seminal fluid is, probably, after the period of puberty, secreted constantly, though, except under excitement, very slowly in the tubules of the testicles. From these it passes along the vasa deferentia into the vesiculæ seminales, whence, if not expelled in emission, it may be discharged, as slowly as it enters them, either with the urine, which may remove minute quantities, mingled with the mucus of the bladder and the secretion of the prostate, or from the urethra in the act of defecation.

The *vesiculæ seminales* have the appearance of out-growths from the vasa deferentia. Each of these ducts, just before it enters the prostate gland, through part of which it passes to terminate in the urethra, gives off a side-branch, which bends back from it at an acute angle; and this branch dilating, variously branching, and pursuing in both itself and its branches a tortuous course, constructs the vesicula seminalis. Each of

the vesiculæ, therefore, might be unravelled into a single branching tube, sacculated, convoluted, and folded up.

The mucous membrane lining the vesiculæ seminales, like that of the gall-bladder, is minutely wrinkled and set with folds and ridges arranged so as to give it a finely-reticulated appearance. The rest of their walls is formed, chiefly, of a layer of organic muscular fibres, from which they derive contractile power for the expulsion of their contents.

To the vesiculæ seminales a double function may be assigned; for they both secrete some fluid to be added to that of the testicles, and serve as reservoirs for the seminal fluid. The former is their most constant and probably most important office; for in the horse, bear, guinea-pig, and several other animals, in whom the vesiculæ seminales are large and of apparently active function, they do not communicate with the vasa deferentia, but pour their secretions separately, though it may be simultaneously, into the urethra. In man, also, when one testicle is lost, the corresponding vesicula seminalis suffers no atrophy, though its function as a reservoir is abrogated. But how the vesiculæ seminales act as secreting organs is unknown; the peculiar brownish fluid which they contain after death does not properly represent their secretion, for it is different in appearance from anything discharged during life, and is mixed with semen. It is nearly certain, however, that their secretion contributes to the proper composition of the impregnating fluid; for, in all the animals in whom they exist, and in whom the generative functions are exercised at only one season of the year, the vesiculæ seminales, whether they communicate with the vasa deferentia or not, enlarge commensurately with the testicles at the approach of that season.

That the vesiculæ are also reservoirs in which the seminal fluid may lie for a time previous to its discharge, is shewn by their commonly containing the seminal filaments in larger abundance than any portion of the seminal ducts themselves do. The fluid-like mucus, also, which is often discharged

from the vesiculæ in straining during defecation, commonly contains seminal filaments. But no reason can be given why this office of the vesiculæ should not be equally necessary to all the animals whose testicles are organized like those of man, or why in any animals the vesiculæ are wholly absent.

There is an equally complete want of information respecting the secretions of the prostate and Cowper's glands, their nature and purposes. That they contribute to the right composition of the impregnating fluid, is shewn both by the position of the glands, and by their enlarging with the testicles at the approach of an animal's breeding time. But that they contribute only a subordinate part is shewn by the fact, that, when the testicles are lost, though these other organs be perfect, all procreative power ceases.

The mingled secretions of all the organs just described form the semen or seminal fluid. Its corpuscles are already described: its fluid part has not been satisfactorily analysed; but Henle says it contains fibrine, because shortly after being discharged, flocculi form in it by spontaneous coagulation, and leave the rest of it thinner and more liquid, so that the filaments move in it more actively.

Nothing has shewn what it is that makes this fluid capable of impregnating the ovum, or (what is yet more remarkable) of giving to the developing offspring all the characters, in features, size, mental disposition, and liability to disease, which belong to the father. This is a fact wholly inexplicable; and is, perhaps, exceeded in strangeness by none but those which shew that the seminal fluid, either directly, or, more probably, through the medium of the mother, may exert such an influence, not only on the ovum which it impregnates, but on many which are subsequently impregnated by the seminal fluid of another male. It has been often observed, for example, that a well-bred bitch, if she have been once impregnated by a mongrel-dog, will not bear thorough-bred puppies in the next two or three litters after that succeeding the copulation with the

mongrel. But the best instance of the kind was in the case of a mare belonging to Lord Monson, who, while he was in India, and wished to obtain a cross-bred between the horse and quagga, caused this mare to be covered by a male quagga. The foal that she next bore had distinct marks of the quagga, in the shape of its head, black bars on the legs and shoulders, and other characters. After this time she was thrice covered by horses, and every time the foal she bore had still distinct, though decreasing, marks of the quagga; the peculiar characters of the quagga being thus impressed not only on the ovum then impregnated, but on the three following ova impregnated by horses. Of the various theories which have been advanced in explanation of this singular fact, of which many parallel instances are on record, none bear so much weight as that recently promulgated by Dr. Alexander Harvey, according to which the constitution of an impregnated female becomes so altered and tainted with the peculiarities of the impregnating male, through the medium of the fœtus, that she necessarily imparts such peculiarities to any offspring she may subsequently bear by other males.*

## DEVELOPMENT.

### *Changes in the Ovum previous to the Formation of the Embryo.*

Of the changes which the ovum undergoes previous to the formation of the embryo, some occur while it is still in the ovary, and are apparently independent of impregnation: others take place after it has reached the Fallopian tube. The knowledge we possess of these changes is derived almost exclusively from observations on the ova of mammiferous animals, espe-

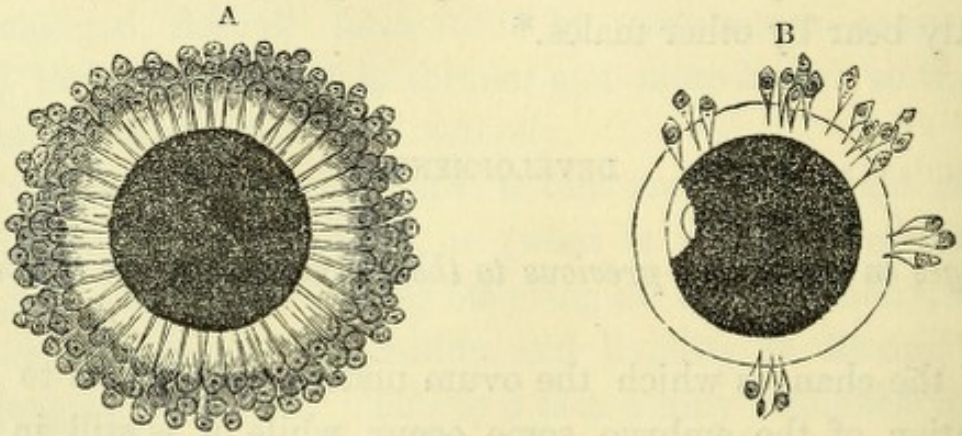
* For an account of Dr. Harvey's important investigations on this subject, the reader is referred to his original papers in the Monthly Journal of Medical Science for 1849 and 1850, or to his Essay on Cross-breeding (cxcix.).

cially the bitch and rabbit: but it may be inferred that analogous changes ensue in the human ovum.

Bischoff (clxxxvii.) describes the yelk of an ovarian ovum after coitus as being unchanged in its characters, with the single exception of being fuller and more dense; it is still granular, as before, and does not possess any of the cells subsequently found in it. The germinal vesicle always disappears, sometimes before the ovum leaves the ovary, at other times not until it has entered the Fallopian tube; but always before the commencement of the metamorphosis of the yelk. Of the manner in which the germinal vesicle, and with it the germinal spot, disappears, and of the changes which they are supposed previously to undergo, much has been written, though little is with certainty known.

The cells of the membrana granulosa, which immediately surround and adhere to the ovum, undergo a peculiar change of form about the time at which the ovum is destined to leave

*Fig.* 74*.




the ovary. They become club-shaped, their pointed extremities being attached to the zona pellucida, so as to give the ovum a stellate appearance (see fig. 74). When the ovum

* Fig. 74.—A. An ovarian ovum from a bitch in heat, exhibiting the elongated form and stellate arrangement of the cells of the discus proligerus or membrana granulosa around the zona pellucida. B. The same ovum after the removal of most of the club-shaped cells.

enters the Fallopian tube, these cells lose their spindle or club-like shape, and become quite round. In the bitch, they continue to invest the ovum in this round shape throughout the whole tract of the Fallopian tube, diappearing only when the ovum reaches the uterus; but, in the rabbit, they wholly disappear at its very commencement.

Besides the disappearance of the germinal vesicle, and, in the rabbit, the disappearance also of the cells of the membrana granulosa, the yelk, in the upper part of the Fallopian tube, no longer completely fills the zona pellucida, but contracts, and leaves a clear space between them.

As the ovum approaches the middle of the Fallopian tube, it begins to receive a new investment, consisting of a layer of transparent albuminous or glutinous substance, which forms upon the exterior of the zona pellucida. It is at first exceedingly fine, and, owing to this, and to its transparency, is not easily recognised: but at the lower part of the Fallopian tube it acquires considerable thickness, and shortly begins to assume the characters of the *chorion*, into which it, together with the zona pellucida, is subsequently converted. At this part of its transit along the Fallopian tube, the ovum remains still unchanged in structure, and no alteration, beyond increased thickness, is perceived in the zona pellucida. A remarkable phenomenon has, however, been noticed by Bischoff in the rabbit about this time, namely the performance by the entire yelk of regular and energetic rotatory movements within the zona pellucida; a phenomenon produced, he says, by the action of vilbratile cilia upon the surface of the yelk.

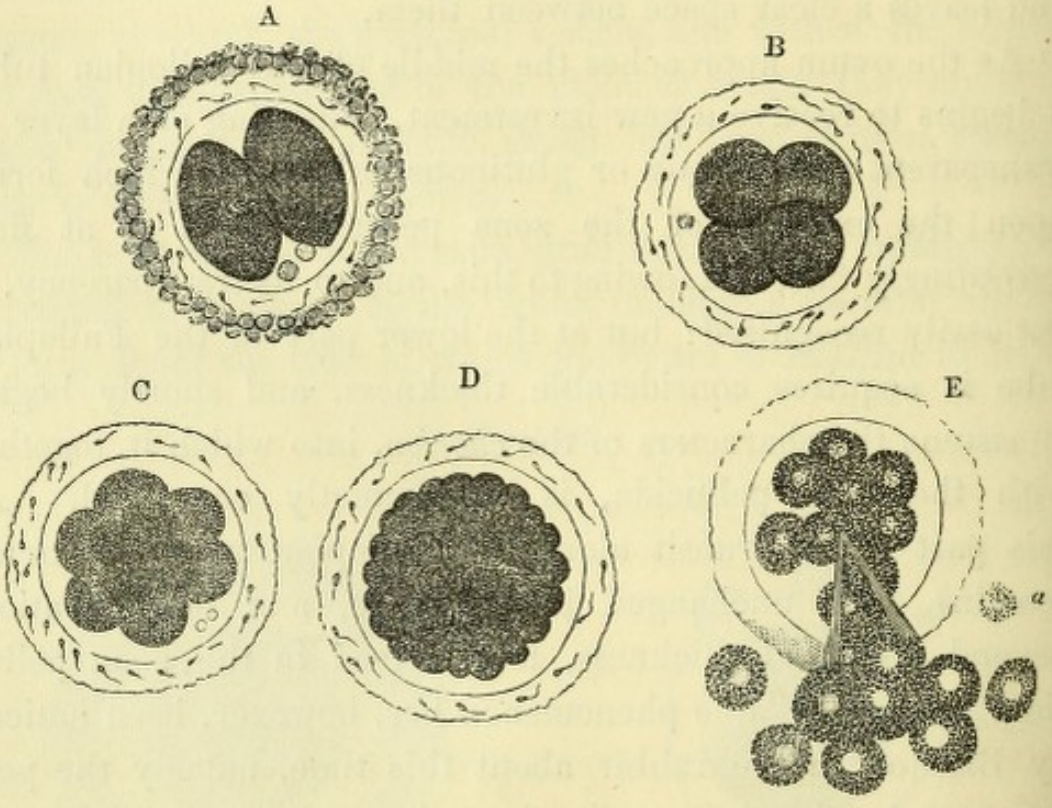
The changes which the mammalian ovum undergoes in its passage through the second half of the Fallopian tube, consist in the further formation of the chorion, and in the peculiar process of *cleaving*, or division and subdivision, of the substance of the yelk, which will now be described.* The

* For an account of the process of cleaving in Amphibia and Fish, see Müller's Elements and the Supplement.

development of the chorion will be considered at a future page.

Bischoff, whose observations were made on rabbits and bitches, states that, when the ovum has passed the middle of the Fallopian tube in its transit to the uterus, the yelk, which was previously one compact uniform mass, begins to be resolved into a number of smaller spheroidal masses; first into two, then into four, then eight, then sixteen, and so on (see fig. 75). Each segment contains a transparent vesicle, like

*Fig. 75.**



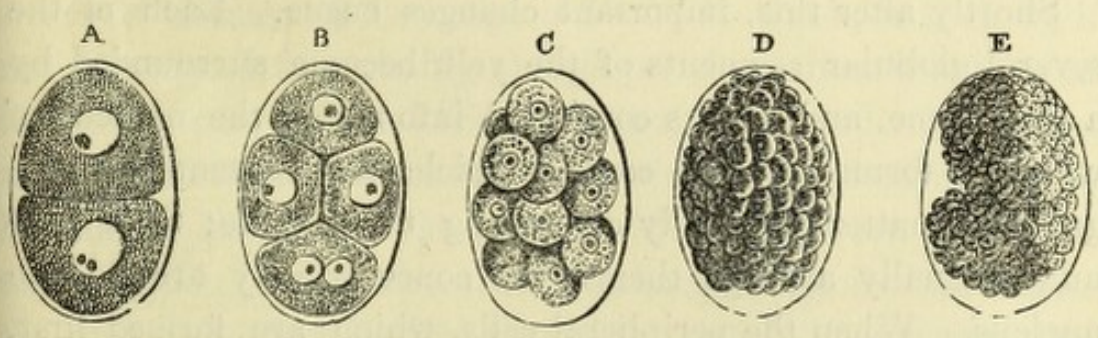

* Fig. 75.—A. Ovum of a bitch, from the Fallopian tube, half an inch from its opening into the uterus, showing the zona pellucida, with adherent spermatozoids, the yelk divided into its first two segments, and two small granules or vesicles contained with the yelk in the cavity of the zona. B. Ovum of a bitch from the lower extremity of the Fallopian tube: the cells of the tunica granulosa have disappeared: the yelk is divided into four segments. C. Ovum of bitch from the lower extremity of the Fallopian tube, in a later stage of the division of the yelk. D. An ovum from the uterus: it is larger, the zona thicker, and the segments of the yelk are very numerous. E. Ovum from the lower extremity of the Fallopian tube burst by compression: the segments of the yelk have partly escaped, and in each of them a bright spot or vesicle is visible.

an oil-globule, which is seen with difficulty, especially in the bitch's ovum, on account of its being enveloped by the yelk-granules, which adhere closely to its surface. He has not been able to detect a nucleus in it, and therefore does not regard it as a true cell. Neither does he regard the globular segments themselves as cells; for neither in the rabbit nor in the bitch can any investing membrane be discerned: they seem to be mere aggregations of yelk-substance around the central body or vesicle.

The cause of this singular subdivision of the yelk is quite obscure: though the immediate agent in its production seems to be the central vesicle contained in each division of the yelk. Originally there was probably but one vesicle, situated in the centre of the entire granular mass of the yelk, and probably derived from the germinal vesicle. This by some process of multiplication, divides and subdivides: then each division and subdivision attracts arounds itself, as a centre, a certain portion of the substance of the yelk.

The process is closely identical with changes which ensue in the ova of certain species of Ascaris, except that, in the latter case, they result from the division and subdivision of

*Fig.* 76.*




* Fig. 76.—Cleaving of the yelk after fecundation. Ascaris nigro-venosa. A. An ovum, the yelk of which is divided into two equal portions; the upper portion contains a cell with a large nucleus; the lower a similar cell with two small nuclei. B. An ovum, of which the yelk is divided into four masses, three of which possess a single nucleated cell, the fourth two such cells. C. An ovum, the globular masses of whose yelk amount to sixteen, in each of which a nucleated cell is clearly dis-

nucleated cells, which, like the oil-like vesicles in the Mammalian ovum, attract around them certain portions of the substance of the yelk (see fig. 76).

About the time at which the mammiferous ovum reaches the uterus, the process of division and subdivision of the yelk appears to have ceased, its substance having been resolved into its ultimate and smallest divisions, while its surface presents a uniform finely-granular aspect, instead of its late mulberry-like appearance. The ovum, indeed, appears at first sight to have lost all trace of the cleaving process, and, with the exception of being paler and more translucent, almost exactly resembles the ovarian ovum; its yelk consisting apparently of a confused mass of finely granular substance. But on a more careful examination, it is found that these granules are aggregated into numerous minute spherical masses, each of which contains a clear vesicle in its centre, but is not, at this period, provided with an enveloping membrane, and possesses none of the other characters of a cell. The zona pellucida, and (in the rabbit) the layer of albuminous matter surrounding it, have at this time the same characters as when at the lower part of the Fallopian tube.

Shortly after this, important changes ensue. Each of the several globular segments of the yelk become surrounded by a membrane, and is thus converted into a cell, the nucleus of which is formed by the central vesicle, the contents by the granular matter originally composing the globule: these granules usually arrange themselves concentrically around the nucleus. When the peripheral cells, which are formed first,

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cernible. After Kölliker (lxxx. 1843). D. and E. are representations of ova from Ascaris acuminata, shewing subsequent steps in the process of division; which goes on until the globular masses become exceedingly small, and are moulded into the form of the young worm. In the late cells, however, the central cells can be no longer recognised. After Bagge (clxxx.)

are fully developed, they arrange themselves at the surface of the yelk into a kind of membrane, and at the same time assume a pentagonal or hexagonal shape from mutual pressure, so as to resemble pavement-epithelium. As the globular masses of the interior are gradually converted into cells, they also pass to the surface and accumulate there, thus increasing the thickness of the membrane already formed by the more superficial layer of cells, while the central part of the yelk remains filled only with a clear fluid. By this means the yelk is shortly converted into a kind of secondary vesicle, situated within the zona pellucida, and named by Bischoff *vesicula blastodermica.*

The vesicula blastodermica, or *germinal membrane*, as it is also called, shortly undergoes a rapid increase in extent and thickness; its growth being effected apparently by the development of new cells, the mode of origin of which is obscure. Within the substance of the germinal membrane shortly appears the first trace of the embryo.

The time occupied in the passage of the ovum, from the ovary to the uterus, occupies, according to Bischoff, three days in the rabbit, four or five days in ruminants, and, probably, eight or ten days in the human female. Bischoff, also, believes that the ovum escapes from the Graafian vesicle at the time when the menstrual discharge is about to cease; and since, if not fecundated, it probably always perishes when it arrives at the lower part of the Fallopian tube, or at any rate, at the uterus, he infers that sexual connection, to be fruitful in the human subject, must take place within eight or ten days from the cessation of the menstrual discharge. Raciborski thinks the time even more limited than this; but he states that impregnation may also result from sexual union taking place one or two days before the commencement of the period of menstruation.*

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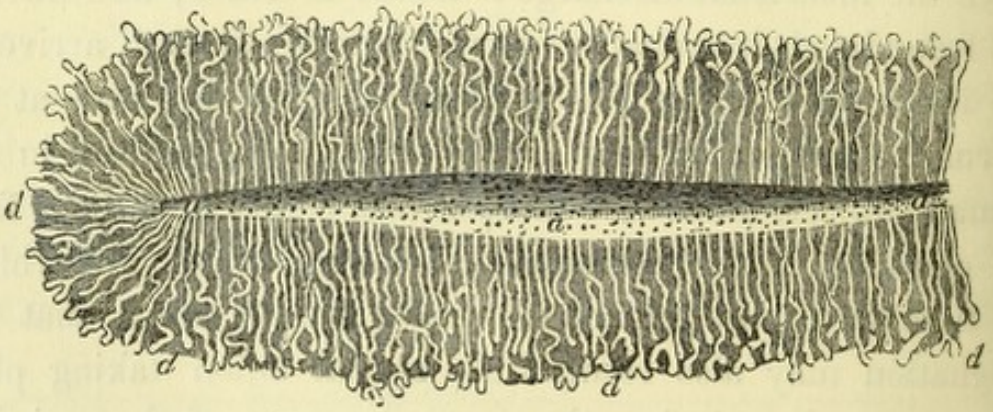
* For a full account of the ovum, see Dr. Allen Thomson's elaborate article on it (lxxiii.).

*Changes of the Ovum within the Uterus.*

It has been remarked, that in its passage along the Fallopian tube the ovum is invested externally with a layer of albuminous substance. In birds, the quantity of this albuminous coating is very large, and constitutes what is termed the *white* of the egg; it serves for the nourishment of the embryo until the chick is fully developed, and ready to maintain its existence out of the shell. Mammiferous ova do not require any such large store of nutriment, for when they reach the uterus they enter into such intimate connection with it, by means of structures presently to be described, that their means of subsistence and growth are derived entirely from the parent.

The exterior of the mammiferous ovum, therefore, acquires only a thin layer of albuminous substance. This shortly becomes intimately united with the zona pellucida, together with which it forms a membrane termed the *chorion*. Shortly after its formation, the chorion sends off from its external surface numerous villous processes, which give it a shaggy or spongy

*Fig.* 77.*

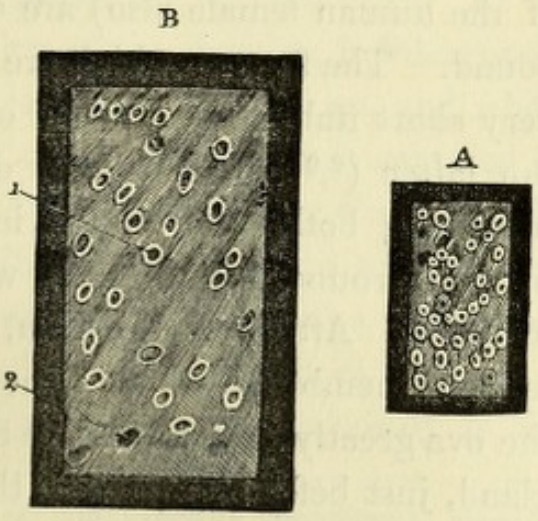



* Fig. 77. Section of the lining membrane of a human uterus at the period of commencing pregnancy, shewing the arrangement and other peculiarities of the glands *d*, *d*, *d*, with their orifices, *a*, *a*, *a*, on the internal surface of the organ. Twice the natural size.

appearance, and which appear to be destined for the absorption of nutriment from the internal surface of the uterus during the earliest period of embryonic life.

Before the impregnated ovum reaches the uterus, certain preparations are made in that cavity for its reception. These changes consist especially in an increased development of the several parts composing the mucous membrane of the uterus, which results in the formation of the *membrana decidua* — so called, on account of being discharged from the uterus at parturition. The mucous membrane of the human uterus is abundantly beset with tubular follicles, arranged perpendicularly to the surface. These follicles are very small in the unimpregnated uterus; but when examined shortly after impregnation, they are found elongated, enlarged, and much waved and contorted towards their deep and closed extremity, which is implanted at some depth in the tissue of the uterus, and commonly dilates into two or three closed sacculi (fig. 77). On the internal surface of the mucous membrane may be seen the circular orifices of the glands, many of which are, in the early period of pregnancy, surrounded by a whitish ring, formed of the epithelium which lines the follicles (fig. 78).

*Fig.* 78.*




Coincidently with the increasing size of the follicles, the quantity of their secretion is augmented, the vessels of the

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* Fig. 78. Two thin segments of human decidua after recent impregnation, viewed on a dark ground; they shew the openings on the surface of the membrane. A is magnified six diameters, and B twelve diameters. At 1 the lining of epithelium is seen within the orifices, at 2 it has escaped. From Dr. Sharpey (xxxii.).

mucous membrane become larger and more numerous, while a substance composed chiefly of nucleated cells fills up the inter-follicular spaces in which the blood-vessels are contained. The effect of these changes is an increased thickness, softness, and vascularity of the mucous membrane, which itself forms the membrana decidua.

The object of this increased development seems to be the production of nutritive materials for the ovum; for the cavity of the uterus shortly becomes filled with secreted fluid, consisting almost entirely of nucleated cells, in which the villi of the chorion are imbedded. The villi of the chorion do not seem to have been ever traced into the follicles, although Bischoff (lxxx. 1847), thinks it probable that they do enter them. But in the bitch they may be easily traced into the dilated glands of the mucous membrane. According to Dr. Sharpey, the glands of the mucous membrane of the bitch's uterus (and, according to H. Müller (cxc. vol. xiii. p. 546) that of the human female also) are of two kinds, simple and compound. The former, which are the more numerous, are merely very short unbranched tubes closed at one end (fig. 79, $^{1},^{1}$); the latter ($^{2},^{2}$) have a long duct dividing into convoluted branches; both open on the inner surface of the membrane by small round orifices, lined with epithelium, and set closely together. After impregnation, the glands of those parts of the mucous membrane which come into immediate relation with the ova greatly enlarge; while the extremity of each compound gland, just before it opens on the surface of the uterus, dilates into a pouch, or cell, filled with whitish secretion, within which is received a process of the chorion. The simple glands also dilate, and receive each a fœtal villus.

When the ovum enters the uterus, it becomes imbedded in the structure of the decidua which is yet quite soft. The earliest ova which have been observed in connection with the decidua, were not contained free in its cavity, but appeared to be implanted in it or pressed into it from without; the decidua, at the point of entrance of the ovum, being protruded

inwards, and the ovum contained in a hollow of its external surface. During the further growth of the ovum, the decidua becomes more and more inverted at this point, the inverted

*Fig.* 79*.

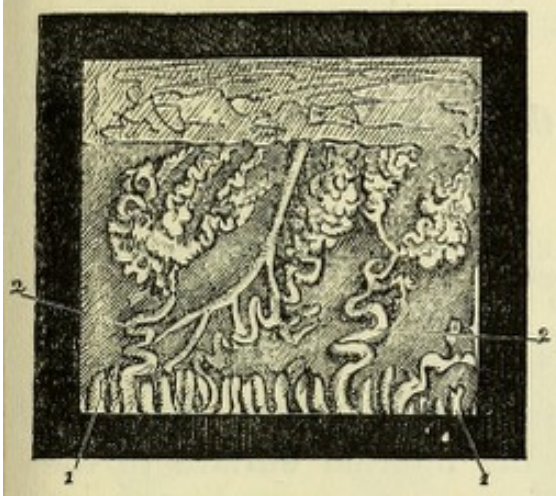
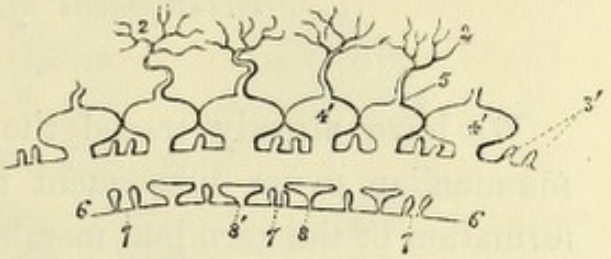



*Fig.* 80.†




part being received into the cavity of the rest of the membrane. This inverted portion is called the *decidua reflexa*,‡ while the other part of the membrane is called the *decidua vera*. At the part where the uterine expansion of the decidua is interrupted by the reflection inwards of the decidua reflexa, and where the ovum entered, the place of the decidua vera is supplied by another layer similar to it, and connected at its margins with it, the "decidua serotina." When young ova are examined in the uterus, both the decidua vera and the decidua reflexa are generally found; but in aborted ova this is seldom the case, a part of the decidua being most frequently retained in the

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* Fig. 79. A vertical section of the mucous membrane, shewing uterine glands of the bitch, magnified twelve diameters: 1, 1, simple glands; 2, 2, compound ditto. From Dr. Sharpey.

† Fig. 80. Diagram of part of the decidua and ovum separated, to shew their mutual relation; 2, compound uterine glands; 3, simple ditto; 4, glandular cells; 5, ducts opening into the bottom of the cells; 6, chorion, 7, villi; 8, 8, fœtal processes of the chorion. From Dr. Sharpey (xxxii.)

‡ The mode in which the decidua reflexa is formed is involved in considerable obscurity. For some of the best observations on the subject, consult Sharpey (xxxii. p. 1580); E. H. Weber (clxxxiii.); Coste (xviii. May, 1847); and Goodsir (ii.)

uterus. As the ovum increases in size, the decidua vera and the decidua reflexa gradually come into contact, and in the third month of pregnancy the cavity between them has quite disappeared. Henceforth it is very difficult, or even quite impossible to distinguish the two layers.

## *Development of the Embryo.*

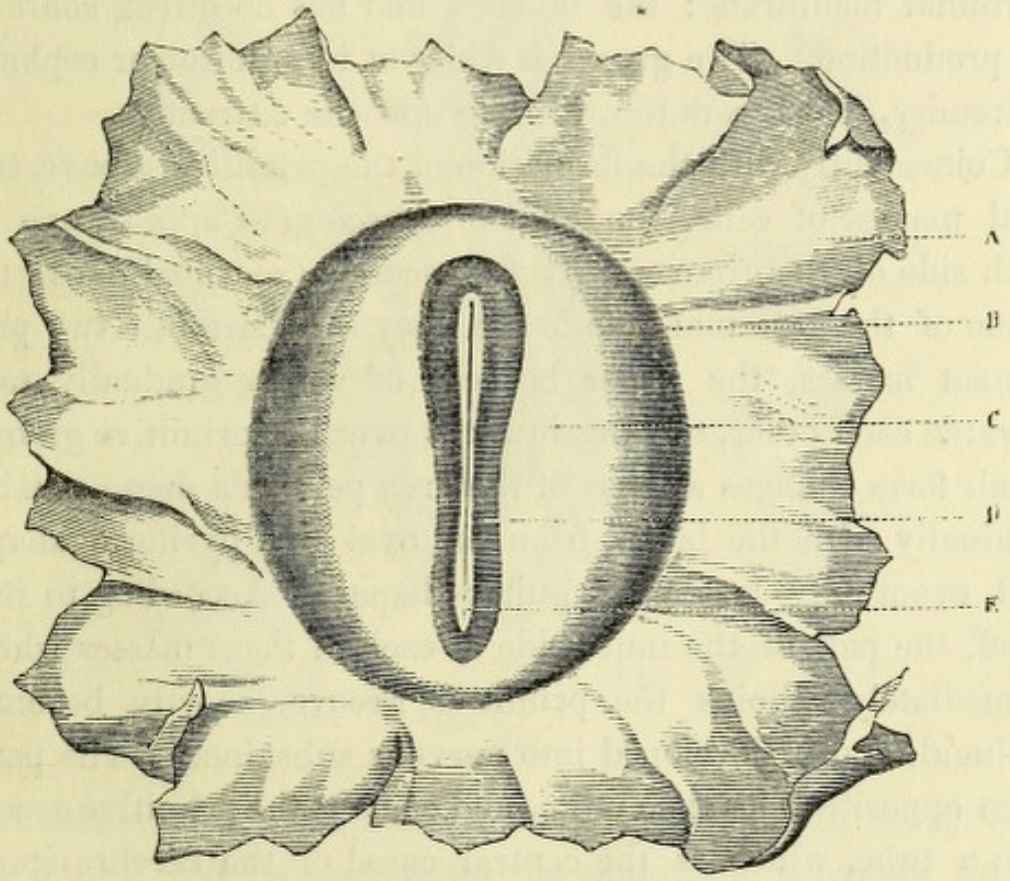
We have already traced the changes which ensue in the mammalian ovum subsequent to impregnation, as far as the formation of the germinal membrane, which consists of a layer of epithelium-like cells enclosing the substance of the yelk, and immediately in contact with the internal surface of the zona pellucida. Most of the subsequent changes which ensue in the formation of the mammalian embryo are similar to those which take place in the development of the chick, and in many respects similar to those which occur in Amphibia and fishes: and the names applied to the several parts are the same in each case. Hence each step in the process may be illustrated by the results of observations on the development of these lower animals.

Very soon after its formation, the germinal membrane presents at one point on its surface an opaque roundish spot, which is produced by an accumulation of cells and nuclei of cells, of less transparency than elsewhere. This space, the "area germinativa" or germinal area, is the part at which the embryo first appears. About the same time the germinal membrane becomes divisible, in the direction of its thickness, into two distinct laminæ. This division is at first most manifest at the situation of the area germinativa; but it soon extends from this point, and implicates nearly the whole of the germinal membrane. The superior or external layer, which lies next to the zona pellucida, is called the *serous layer;* from it are developed the organs of the animal system of the body, *e.g.*, the bones, muscles, and integuments: the inferior or internal division, in

contact with the yelk itself, is named the *mucous layer*, and serves for the formation of the internal or visceral system of organs.

At its first appearance, the area germinativa has a rounded form, but it soon loses this and becomes oval, then pear-shaped,

*Fig.* 81.*




and while this change in form is taking place, there gradually appears in its centre a clear space or *area pellucida* (fig. 81, c), bounded externally by a more opaque circle, which subsequently becomes the *area vasculosa* (B),—so named because of its being the part in which blood-vessels are first formed. In the formation of these two spaces, both the serous and mucous laminæ of the germinal membrane take part. The comparative

* Fig. 81. Portion of the germinal membrane of a bitch's ovum, with the area pellucida and rudiments of the embryo; magnified ten diameters. A. Germinal membrane. B. Area vasculosa. C. Area pellucida. D. Laminæ dorsales. E. Primitive groove, bounded laterally by the pale pellucid substance of which the central nervous system is composed. After Bischoff (clxxxiv.).

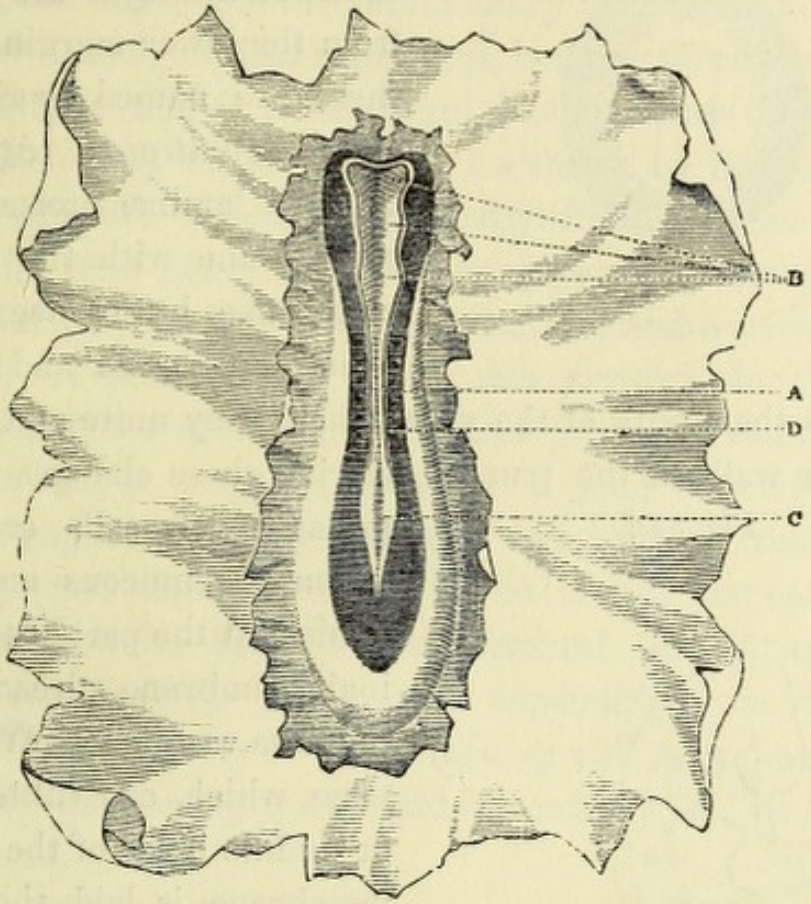
obscurity of the outer space—the area vasculosa—is due to the greater accumulation of nucleated cells and nuclei at that part than in the area pellucida.

The first trace of the embryo in the centre of the area pellucida consists of a shallow groove or channel, the *primitive groove* (fig. 81, E), formed in the external or serous fold of the germinal membrane: the mucous fold has no direct share in its production. The groove is wider at its anterior or cephalic extremity, and tapers towards the opposite extremity.

Coincidently with the formation of the primitive groove, two oval masses of cells, the *laminæ dorsales* (D) appear, one on each side of the groove. At first scarcely elevated above the plane of the germinal membrane, they soon rise into two prominent masses, the upper borders of which gradually tend towards each other, turning inwards over the primitive groove. Their form changes as that of the area pellucida does; passing gradually with the latter from an oval to a pyriform shape, and eventually becoming guitar-shaped. According to Bischoff, the part of the inner side of each of these masses which immediately adjoins the primitive groove, shortly becomes pellucid, and is developed into nervous substance. The parts from opposite sides then unite, and convert the primitive groove into a tube, which is the central canal of the cerebro-spinal axis, the surrounding nervous matter constituting the substance of the rudimental spinal cord and brain or cerebral vesicles, which are thus the first parts of the embryo that are developed. The shaping-out of the three cerebral vesicles or divisions of the brain takes place before the primitive groove is closed over; its cephalic extremity dilating into three pouches (B, fig. 82). The opposite or caudal extremity of the groove at the same time dilates into a lancet-shaped pouch (the sinus rhomboidalis) which corresponds to the future cauda equina (C). The closure of the canal by means of the internal nervous sides of the laminæ dorsales commences first at the middle, and then gradually proceeds along its whole length: at the same time the other parts of the corresponding laminæ dorsales of

the opposite side unite and form the rudiments of the head and dorsal part of the body.

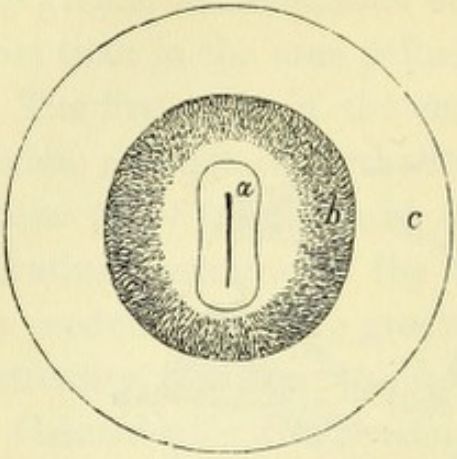
*Fig.* 82.*




Immediately beneath, and in a line parallel with the primitive groove may be seen, about the same time, a narrow linear mass of cells, the *chorda dorsalis*, which forms the basis around which the vertebral column is developed. The development of this column is early indicated by the appearance of a few square, at first indistinct, plates, the rudiments of vertebræ (fig. 82, D), which begin to appear at about the middle of each dorsal lamina.

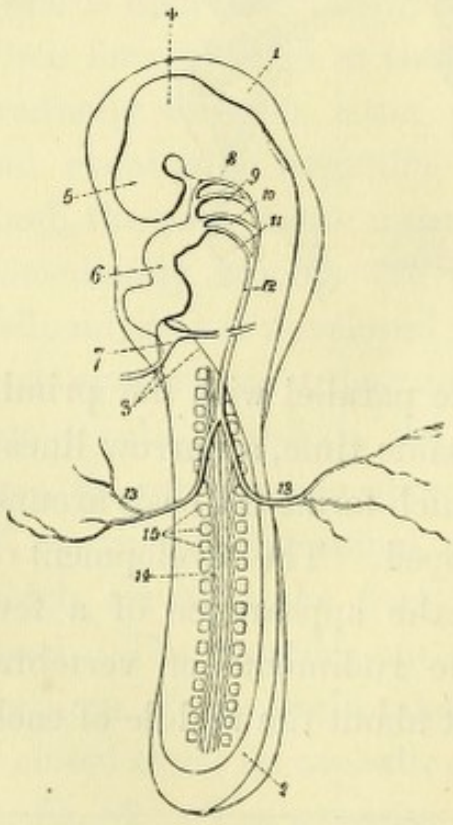
* Fig. 82. Portion of the germinal membrane, with rudiments of the embryo; from the ovum of a bitch. The primitive groove, A, is not yet closed, and at its upper or cephalic end presents three dilatations B, which correspond to the three divisions or vesicles of the brain. At its lower extremity the groove presents a lancet-shaped dilatation (sinus rhomboidalis) C. The margins of the groove consist of clear pellucid nerve-substance. Along the bottom of the groove is observed a faint streak, which is probably the chorda dorsalis. D. Vertebral plates. After Bischoff.

*Fig.* 83.*




While the dorsal laminæ are closing over the primitive groove, thickened prolongations of the serous layer are given off from the lower margin of each; these are named *laminæ viscerales seu ventrales.* At first the visceral laminæ proceed on the same plane with the germinal membrane, but by degrees, they bend downwards and inwards, towards the cavity of the yelk, where they unite and form the anterior walls of the trunk. During these changes an accumulation of cells ensues between the mucous and serous laminæ at the part of the germinal membrane already named the area vasculosa. Within this mass, which constitutes a third or middle layer of the germinal membrane, is laid the foundation for the development of the vascular system. At the circumference of the vascular area, insulated red spots and lines make their appearance, and these soon unite so as to form a net-work of vessels filled with blood (fig. 83). The margin of the vascular layer is at first limited and quite circular,

*Fig.* 84.†



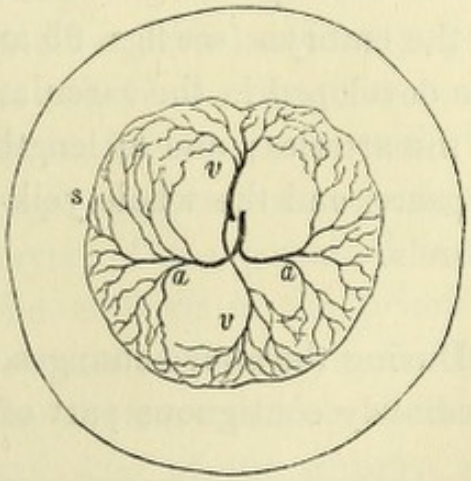

* Fig. 83. Diagram shewing vascular area in the chick. *a.* Area pellucida. *b.* Area vasculosa. *c.* Area vitellina.

† Fig. 84. Embryo of the chick at the commencement of the third day, as seen from the abdominal aspect. After Wagner. 1, involucrum capitis; 2, involucrum caudæ; 3, passage of involucrum capitis into germinal membrane; 4, prominence of the corpora quadrigemina or optic lobes of

being bounded by vessels united in a *circulus venosus*, or *sinus terminalis* (fig. 85), but it soon extends over the whole surface of the germinal membrane.

About the same time the rudimentary heart is formed in the same layer of the germinal membrane, bending downwards from the cephalic portion of the embryo, so as to enclose the anterior part of the cavity of the body. As shewn by Schwann, the blood-vessels are developed originally from nucleated cells. These cells send out processes; the processes from different cells unite; and in this way ramifications and a network are produced. Vessels extend from this network in the area vasculosa into the area pellucida, and join the rudimentary heart. It has, at first, the form of a long slightly-curved tube, prolonged inferiorly into the two venous trunks, and superiorly into three or more aortic arches on each side. These arches unite beneath the vertebral column and form the aorta (see fig. 84). The vessels extending from the vascular layer now ramify in the animal, as well as in the organic, system of the embryo, and aid essentially in its further development.

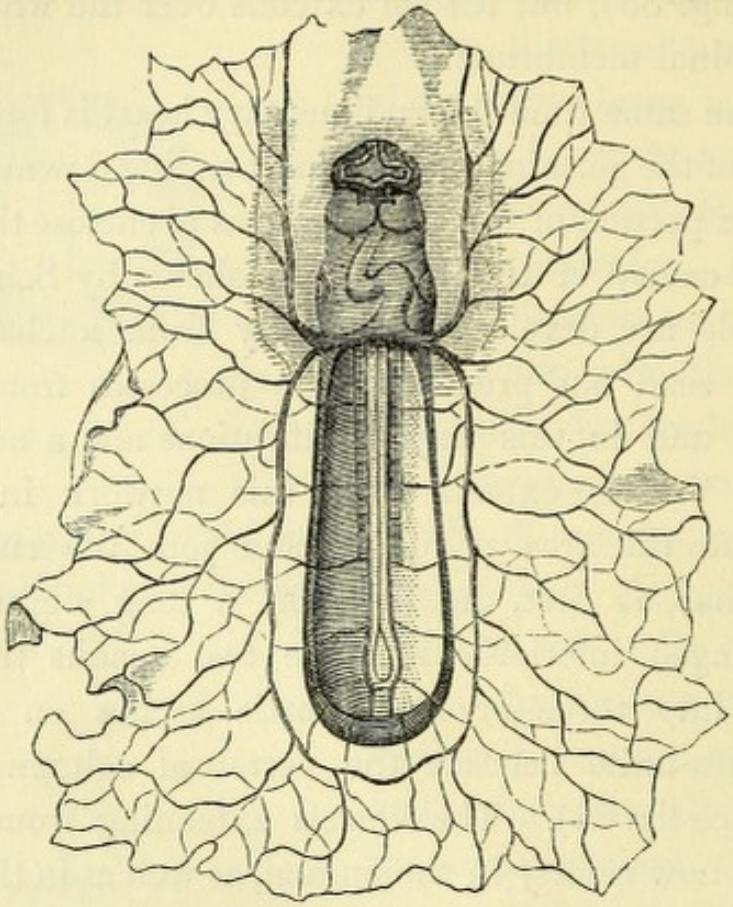
*Fig.* 85.




In the primitive state of the embryonic circulation, the aorta divides into a right and a left branch, and these are continued as the *arteriæ omphalo-mesentericæ* (*a*, *a*, fig. 85), into the germinal membrane, where they ramify and anastomose until they reach a circular venous canal (*s*) which surrounds the area vasculosa. From this venous canal, the

the brain; 5, the anterior cerebral mass or hemispheres; 6, the heart; 7, entrance of the great venous trunks in the atrium cordis or auricle; 8, 9, 10, and 11, the four aortic arches; 12, the descending aorta; 13,the arteries of the germinal membrane; 14, the dorsal laminæ, rendered slightly wavy by the action of water; 15, the rudiments of the vertebræ.

*Fig.* 86.*



*sinus terminalis*, and from the vascular network of the germinal membrane, the blood is brought back by the *venæ omphalo-mesentericæ* (*v*, *v*), which issue from the area vasculosa at points corresponding to the anterior and posterior extremities of the embryo (see figs. 85 and 86). Subsequently other veins are developed in the vascular network, which follow the course of the arteries; and at length the terminal sinus entirely disappears, and the whole yelk-sac becomes covered with blood-vessels.

During the above changes, the embryo, together with the immediately contiguous part of the germinal membrane, elevates

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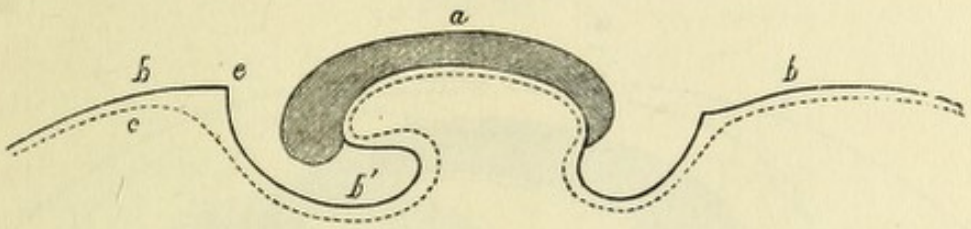
* Fig. 86. Embryo from a bitch at the 23rd or 24th day, magnified ten diameters. It shews the net-work of blood-vessels in the vascular lamina of the germinal membrane and the trunks of the omphalo-mesenteric veins entering the lower part of the S-shaped heart. The first part of the aorta is also seen. After Bischoff.

itself above the level of the rest of that membrane in the form of a small boat (see fig. 87), enclosing a cavity open beneath,

*Fig.* 87.*




which is the first condition of the cavity of the trunk of the future animal. The cephalic end of the embryo, with the anterior part of the body, first bends forwards and downwards. and the germinal membrane follows this depression, producing a fold termed the *involucrum capitis*. Shortly afterwards, a similar fold of the germinal membrane is formed at the caudal extremity of the embryo (*vagina caudæ*), and presses from behind forwards beneath it (fig. 87). These two folds are connected by that part of the boat-shaped embryo which passes off from the structures of the axis on each side into the expanded germinal membrane. In this way, the embryo becomes in some measure separated by constriction, both anteriorly, posteriorly, and at the sides, from the rest of the germinal membrane, above the surface of which it elevates itself, with the cavity of its trunk, still in great part open, turned towards the yelk. The part of the internal layer of the germinal membrane which lines the cavity of the embryo is the primitive form of the intestinal canal. That part of the external layer of the germinal membrane, on the contrary, which descends on each side from the rudimentary axis of the embryo, and

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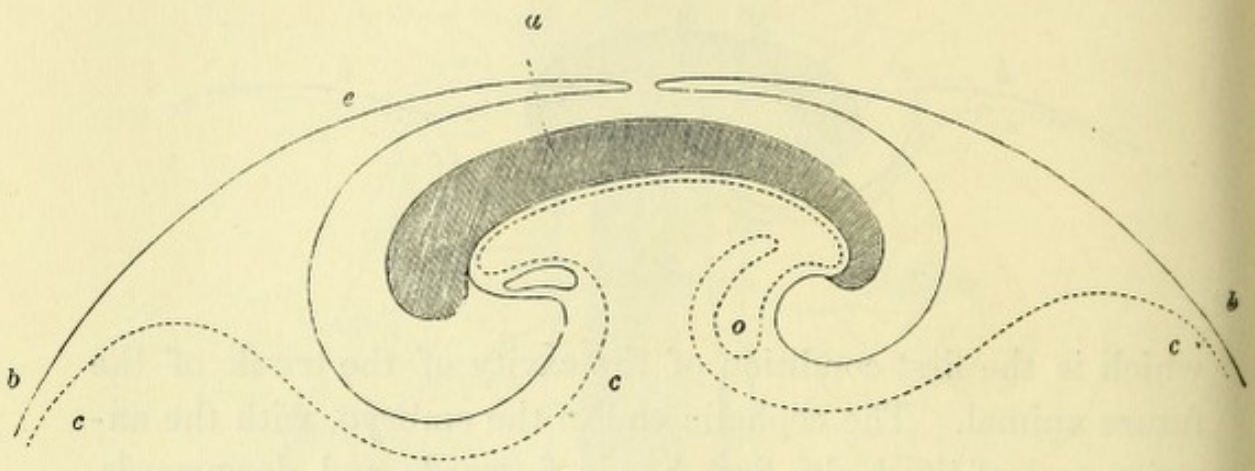
* Fig. 87. A longitudinal section of an embryo chick in the second day of incubation. *a*, section of the embryo; *b*, the external layer of the germinal membrane; *c* the internal layer; *b'*, the involucrum capitis.

contributes to its boat-like form, is continuous with the rudimentary structures which are destined to form the parietes of the trunk, namely, the walls of the neck, chest, and abdomen.

*Fig.* 88.



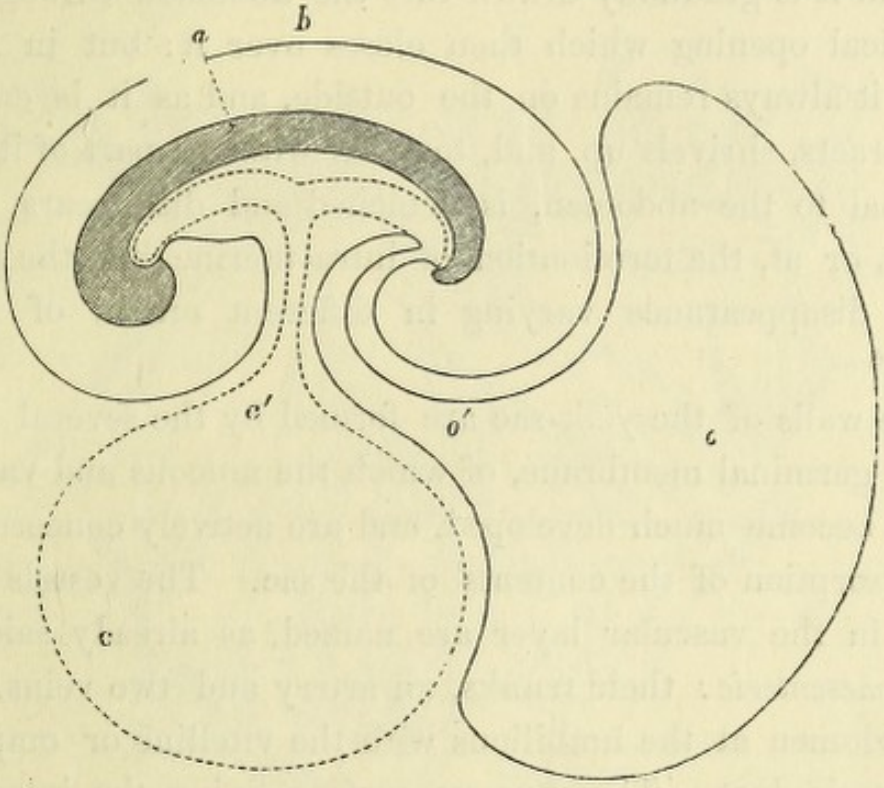

In further continuation of the above changes, the cephalic, caudal, and lateral edges of the external layer of the germinal membrane rise still more, and extend over the body of the embryo from its abdominal towards its dorsal aspect, where they at length meet and coalesce, enclosing the embryo in a shut sac, the *amnion* (figs. 88 and 89).

While the inner of the two layers of which this fold of the germinal membrane consists forms the sac of the amnion, the outer lines the internal surface of the zona pellucida, or, as it has now become, the chorion. The lamella forming the amnion is continuous with the skin of the embryo at the former line of union of the parietes of its body with the external layer of the germinal membrane. The parietes of the body of the embryo are therefore reflected upon themselves, as it were, so as to form the membrane of the amnion. The part at which the reflection takes place is the *umbilicus*. This, at first, is wide and long, but it gradually grows smaller.

The inner layer of the germinal membrane remains continuous with the intestinal cavity. The constricted part at which it is continued into the wall of the intestinal cavity or tube (fig. 88, *c'*) is now called the *vitelline duct*, *ductus vitello-in-*

*testinalis*, or omphalo-mesenteric duct; the inner layer of the germinal membrane having at this period extended over the whole yelk, and become the *vitelline sac, yelk-sac,* or, in Mammalia, the *umbilical vesicle.*

*Fig.* 89.*




By the constriction which the fold of germinal membrane, in which the abdominal walls are formed, produces at the umbilicus (*c'*), the body of the embryo becomes in great measure detached from the yelk-sac or umbilical vesicle, though the cavity of the rudimentary intestine still communicates with it through the vitelline or omphalo-mesenteric duct, and contains part of the yelk-substance with which the vesicle was filled. The yelk-sac contains, however, the greater part of the substance of the yelk, and furnishes a source whence nutri-

* In figure 89, *a* represents the dorsal structures of the embryo; *b*, the amnion; *c*, the yelk-sac or umbilical vesicle; *c'*, the vitelline duct or pedicle of the umbilical vesicle; *o*, the allantois; and *o'*, the urachus.

ment is derived for the embryo. In birds, the contents of the yelk-sac afford nourishment until the end of incubation: but in Mammalia, the office of the corresponding umbilical vesicle ceases at a very early period, the quantity of yelk is small, and the embryo soon becomes independent of it by the connections it forms with the parent. Moreover, in birds, as the sac is emptied it is gradually drawn into the abdomen through the umbilical opening which then closes over it: but in Mammalia it always remains on the outside, and as it is emptied it contracts, shrivels up, and, together with the part of its duct external to the abdomen, is detached and disappears either before, or at, the termination of intra-uterine life, the period of its disappearance varying in different orders of Mammalia.*

The walls of the yelk-sac are formed by the several layers of the germinal membrane, of which the mucous and vascular layers become much developed, and are actively concerned in the absorption of the contents of the sac. The vessels ramifying in the vascular layer are named, as already said, *omphalo-mesenteric:* their trunks, an artery and two veins, enter the abdomen at the umbilicus with the vitelline or omphalo-mesenteric duct. The mucous surface lining the interior of the sac is, in the chick, especially, highly developed, and presents numerous vascular folds or processes for the absorption of the yelk; for the contents of the sac do not pass directly into the intestine, with which at first, through the pervious vitelline duct, the sac communicates, but are absorbed by the omphalo-mesenteric vessels, and conveyed to the liver. The vascular folds of the mucous membrane are covered by the granules of the yelk which give them a yellowish colour, and hence led to the vessels being formerly called *vasa lutea.**

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* For a minute account of the structure and office of the mucous coat of the umbilical vesicle of the chick by Mr. Grainger, see Müller (xxxii. p. 1557).

During the formation of the umbilical vesicle a pear-shaped solid mass of cells projects from the inferior or caudal extremity of the embryo, and is shortly developed into a vesicle

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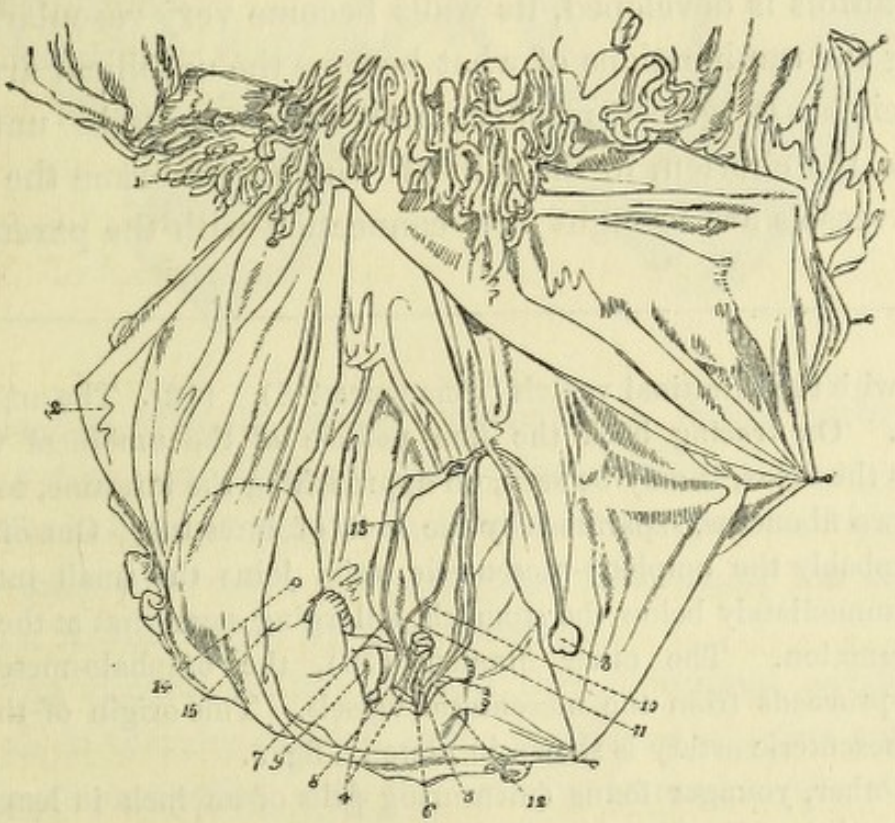
The blood-vessels of the umbilical vesicle (omphalo-mesenteric vessels) are well shewn in the preparation of a human embryo belonging to



Dr. Sharpey (plate iii.). The annexed figure is an outline copy of the plate referred to. The aborted ovum measured about 1½ inch. Abundant and large villi extended from the chorion (1) to the decidua at the part where the cord was attached. The amnion (2) is laid open, and the fœtus lies at the bottom of its cavity. The vesicula umbilicalis (3), rather more than $\frac{1}{10}$th of an inch in diameter, adheres to the outside of the amnion, connected by its pedicle to the umbilical cord. The intestine (4) on leaving the stomach makes a turn to the right; then, after a retrograde bend, passes through the umbilicus into the cord, at first straight (5), then making three coils in the cord, then returning straight again (6) into the abdomen, and terminating at the lower end of the body. The straight returning portion is the large intestine, as indicated by the commencing cæcum which appeared at the point where the coils within the cord terminated (see plate iv. fig. 5). The umbilical vein (7) may be easily traced to the lower part of the liver (9), being there con-

named *allantois*. It has been said by some to proceed directly from the intestinal canal (as represented in fig. 89); by others from the Wolffian bodies or rudimental kidneys; but, at least in the Mammalia, it does not do so, for, as shewn by Bischoff, at the time of its first appearance, no trace either of the intestinal canal or of the Wolffian bodies can be perceived. It subsequently, however, communicates with both these parts. As the allantois is developed, its walls become very vascular, containing the ramifications of what become the umbilical arteries and vein. It grows rapidly, and elongates itself until it reaches the chorion, in the villi of which membrane the umbilical vessels are brought into connection with the parent by

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nected with the intestinal vessels (vena portæ? 8). (12). The umbilical arteries. On tracing back the fine pedicle of the umbilical vesicle towards the fœtus, it may be seen, on approaching the intestine, to consist of two filaments, separated by the coil of intestine. One of these (11), probably the omphalo-mesenteric vein, joins the small intestine almost immediately below the stomach, enlarging somewhat at the point of its junction. The other filament (10), the omphalo-mesenteric artery, proceeds from the mesenteric vessels. This origin of the omphalo-mesenteric artery is shewn in plate iv. fig. 5.

In another, younger fœtus (measuring $\frac{6}{10}$ths of an inch in length) in the possession of Dr. Sharpey, the filament which appears to be identical with the omphalo-mesenteric vein was traced further into the abdomen, —namely, beneath the intestine to the membrane, and probably to the vessels, which lie in the concavity of the first intestinal turn. This fœtus is represented in fig. 4, plate iv. The canal of the intestine has been cut transversely, and the minute filament or vessel is seen passing beneath it.

Figs. 1, 2, and 3, plate iii. are drawings of an ovum and embryo at the thirty-fourth day. The ovum was seven lines in diameter; the embryo two and a half lines in length. The intestine consisted of a canal opening by a very wide orifice into the umbilical vesicle at the point where the abdominal lamina is reflected into the amnion; so that, in the situation of the future duct of the vesicle, there was merely a slight constriction. The embryo had three pairs of branchial clefts and arches, behind which, in the middle line, and projecting from the anterior face of the embryo, was situated the tubular heart (see fig. 2). After Müller.

means of the *placenta*, presently to be described. In Mammalia, the vessels conveyed by the allantois are distributed only at that part in which the placenta exists; but in birds,

*Fig.* 90.*

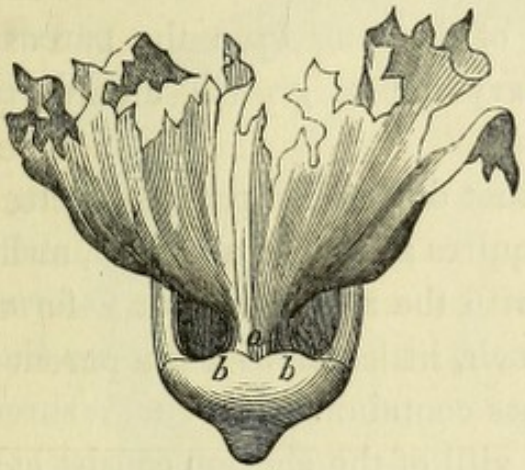
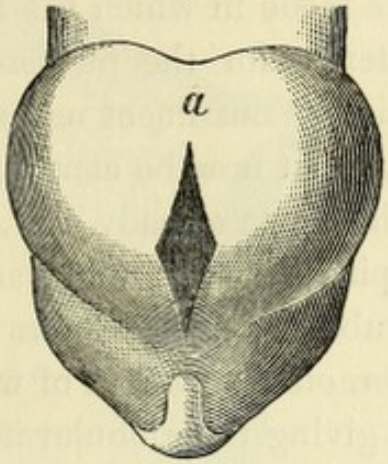



*Fig.* 91.†




the allantois with its vessels envelopes the entire embryo; it forms a very vascular layer lining the interior of the egg-shell, and affords by this means an extensive surface in which the blood may be aërated. In placental Mammalia the aërating function is discharged by the placenta.

As the visceral laminæ close-in the abdominal cavity, the allantois is thereby divided at the umbilicus into two portions: the larger proceeding with the umbilical vessel to the chorion, while the smaller is retained in the abdomen, and converted into the urinary bladder. These two portions are connected together by a constricted part, named the *urachus*.

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* Fig. 90. The lower part of the body of a bitch's embryo, magnified ten diameters. The mucous and vascular layers of the germinal membrane are turned back to shew (*a*) the pedicle of the umbilical vesicle at its entrance into the abdominal cavity. *b*, *b*. The two cellular masses out of which (in the bitch) the allantois is formed. After Bischoff.

† Fig 91. The lower extremity of an older embryo. The allantois (*a*) is developed into a single vesicle, but its origin from two symmetrical halves is still shewn, especially by the fissure in the middle. (Ibid.)

## *The Chorion and Placenta.*

The mode in which the human embryo is connected with the uterus, for the purpose of drawing from the parent the supplies of nutriment necessary for its growth and development, must now be considered.

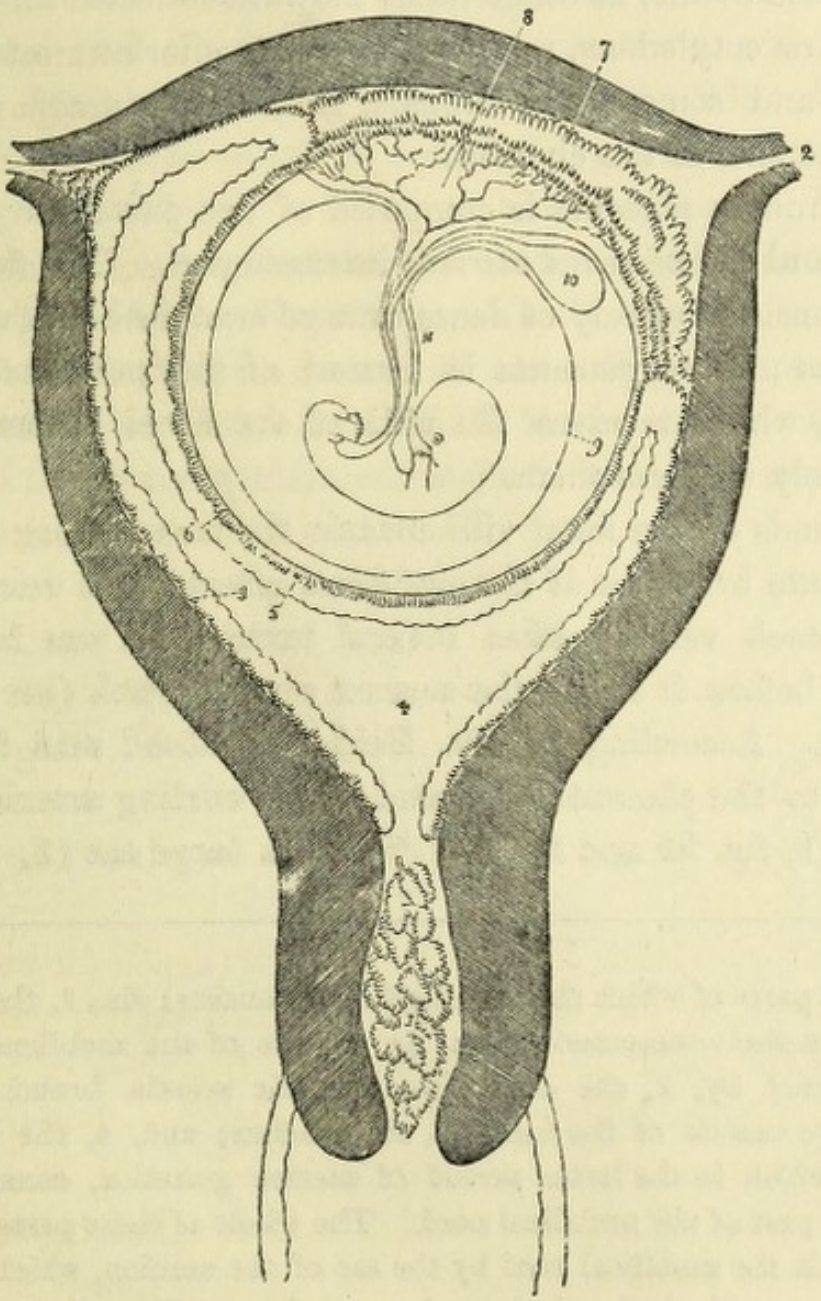
It has been already said, that during its passage along the Fallopian tube, the ovum acquires a layer of albumen, and that this subsequently coalesces with the zona pellucida to form the *chorion*, on the surface of which, little villous processes shortly arise, giving the globular mass containing the ovum a shreddy, flocculent appearance. The villi of the chorion consist at first entirely of cells bounded by an external layer of textureless membrane, which gives their form (Goodsir). When the ovum, with its villous chorion, reaches the uterus, the villi become imbedded in the secretion poured forth by the enlarged follicular glands of the mucous membrane of that organ; and from this they doubtless derive the nutriment on which the embryo at first subsists.

Further provision is, however, shortly made for procuring nourishment, by the development of blood-vessels within the villi, and the junction of these with the branches of the umbilical vessels brought by the allantois to the chorion. The fœtal vessels thus come into intimate relation with the vessels of the uterus. The part at which this relation between the vessels of the fœtus and those of the parent ensues is not, however, over the whole surface of the chorion; for, although all the villi become vascular, yet, in the human subject, it is at one part only that they are greatly developed, and by their branching give rise, with the vessels of the uterus, to the formation of the *placenta* (fig. 92).

The ovum appears to have a firm connection with the uterus in all Mammalia, with the exception of the Marsupialia and Monotremata. The means of attachment are always either

vascular villi or folds of the chorion. The chorion receives its blood-vessels from the umbilical vessels of the fœtus, which

*Fig.* 92.*



* Fig. 92 represents a perpendicular section of a uterus, with a fully formed ovum. A plug of lymph (1) occupies the cervix uteri; 2, indicates the opening of the Fallopian tube on one side; 3, the decidua vera 4. the cavity of the uterus nearly filled by the ovum; 5, the decidua reflexa; 6, the chorion; 7, the decidua serotina (see p. 645); 8, the allantois and the situation of the future placenta; 9, the amnion; 10, the umbilical vesicle; 11, the umbilical cord. An examination of the above diagram, with the remembrance of what has been said before, will ex-

are distributed upon the allantois, and by it are conducted to the chorion. The villi are sometimes distributed over the whole surface of the chorion; sometimes they form a zone around the ovum; at other times they are collected into several masses, or cotyledons, scattered over the chorion; and lastly, in man and some other animals, they form a single placenta upon one side of the chorion.

The human placenta is composed of two parts, the *placenta fœtalis* and the *placenta uterina*, intermingled. The fœtal placenta consists entirely of dense tufts of branched vascular villi, while the uterine placenta is formed of the substance of the decidua, which receives the villi of the fœtal placenta, and completely encloses them.

The ends of the fœtal villi contain the inosculating loops of the minute branches of the umbilical arteries and veins of the fœtus; each vessel makes several turns from one loop into another before it enters the nearest venous trunk (see figs. 93 and 94). According to Dr. Reid, the blood sent from the mother to the placenta is poured by the curling arteries of the uterus (1, fig. 95 and fig. 96) "into a large sac (3, fig. 96)

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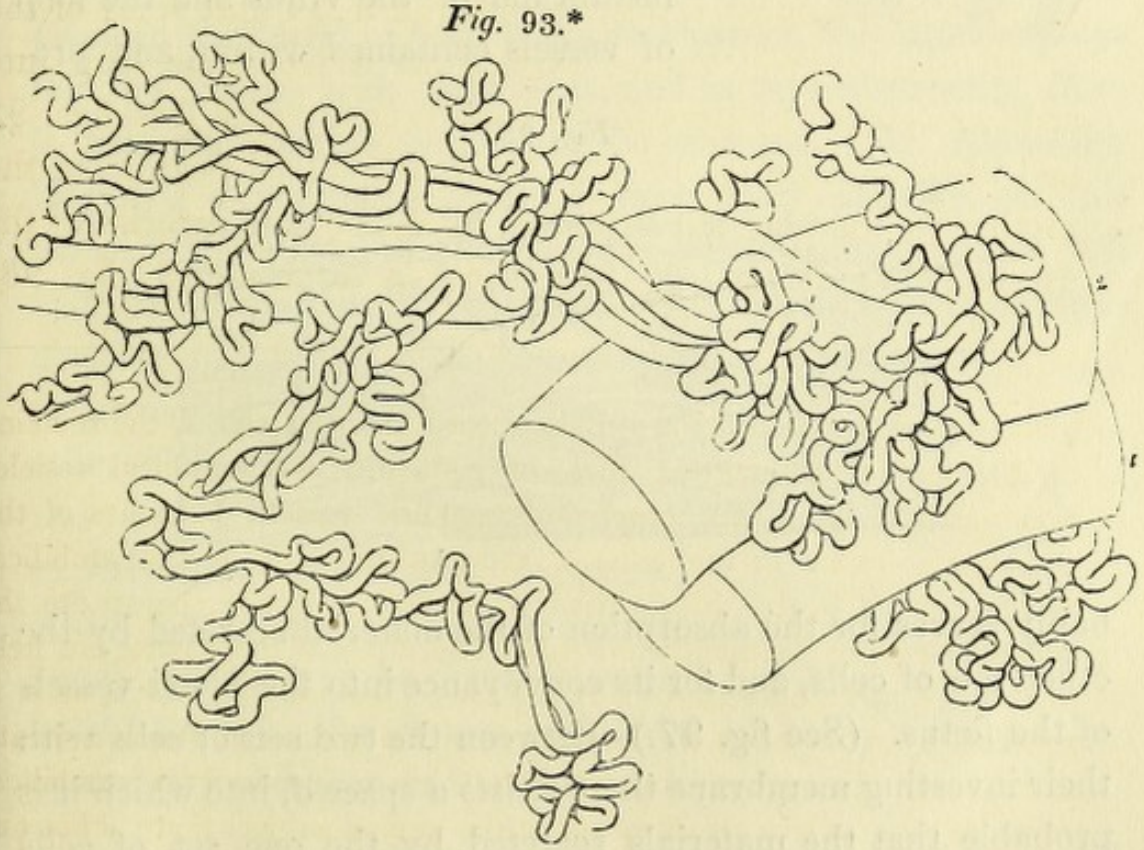
plain the parts of which the umbilical cord consists: viz., 1, the remains of the omphalo-mesenteric duct, or pedicle of the umbilical vesicle; accompanied by, 2, the omphalo-mesenteric vessels, branches of the mesenteric vessels of the fœtus; 3, the urachus; and, 4, the umbilical vessels, which in the latter period of uterine gestation, constitute the principal part of the umbilical cord. The whole of these parts are held together in the umbilical cord by the sac of the amnion, which, as it is reflected upon the body of the embryo at the umbilicus, forms a sheath to the cord. In mammiferous animals, there are generally two umbilical veins, as well as two arteries; but in the human subject there is but one umbilical vein, with two umbilical arteries. The umbilical arteries are the main branches of the internal iliac arteries. They convey the blood of the fœtus into the placenta, whence it is returned by small veins, which by their union form the umbilical vein. The umbilical vein, of which the persistent vena abdominalis of reptiles and Amphibia is the analogue, pours its blood partly into the vena portæ, and partly, through the ductus venosus, into the vena cava.

formed by the inner coat of the vascular system of the mother, which is intersected in many thousand different directions by the placental tufts (4, fig. 95), projecting into it like fringes, and pushing its thin wall before them in the form of sheaths, which closely envelope both the trunk and each individual branch composing these trunks (fig. 96). From this sac the maternal blood is returned by the utero-placental veins (2, fig. 96)."

It thus appears, that the tufts and villi of the fœtal portion of the placenta are completely ensheathed by the lining membrane of the vascular system of the mother. It would seem, also, from the observations of Professor Goodsir, that, at the villi of the placental tufts, where the fœtal and maternal portions

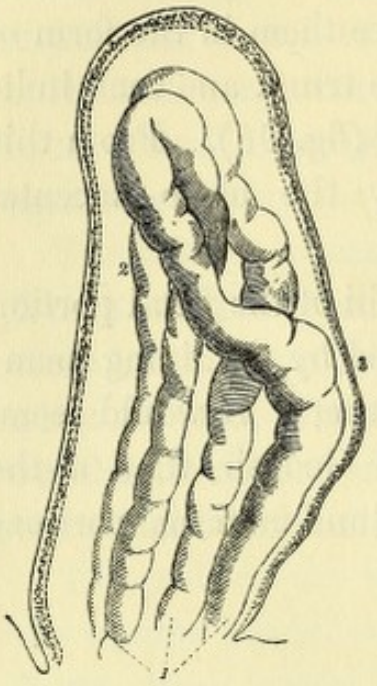
*Fig.* 93.*



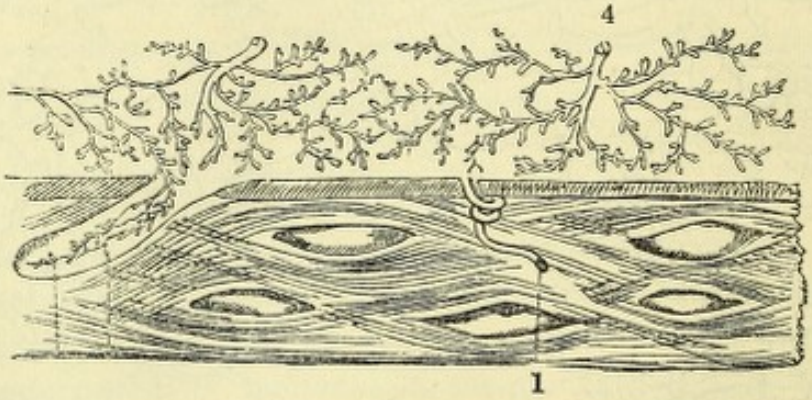
* Fig. 93 represents the villi of the fœtal portion of a mature human placenta, magnified 100 diameters. After E. H. Weber. The capillary vessels are filled with injection, and their diameter varies from $\frac{1}{113}$ to $\frac{1}{170}$ of a French line. 1, the artery; 2, the vein.

of the placenta are brought into close relation with each other, the blood in the vessels of the mother is separated from that in the vessels of the fœtus by the intervention of two distinct sets of nucleated cells. One of these belongs to the maternal portion of the placenta, is placed between the membrane of the villus and that of the vascular system of the mother, and is probably designed to separate from the blood of the parent the materials destined for the blood of the fœtus; the other belongs to the fœtal portion of the placenta, is situated between the membrane of the villus and the loop of vessels contained within, and probably serves for the absorption of the material secreted by the other sets of cells, and for its conveyance into the blood-vessels of the fœtus. (See fig. 97.) Between the two sets of cells with their investing membrane there exists a space *d*, into which it is probable that the materials secreted by the one set of cells of the villus are poured, in order that they may be absorbed

*Fig.* 94.*



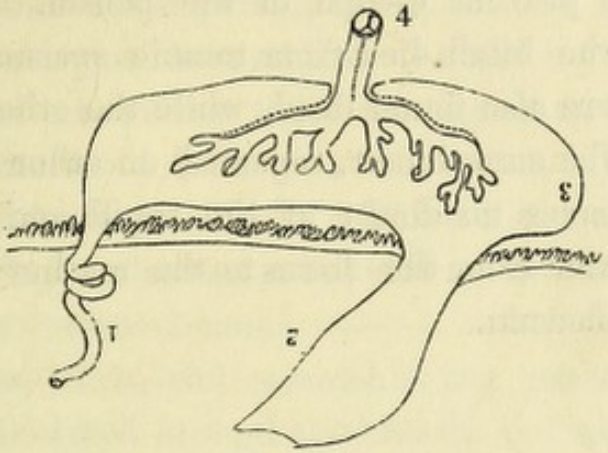

*Fig,* 95.




* Fig. 94 is the extremity of a villus magnified 200 diameters. After Weber. The loop, 1, is filled with blood; the other loop, 2 is empty; 3, is the margin of the pellucid villus.

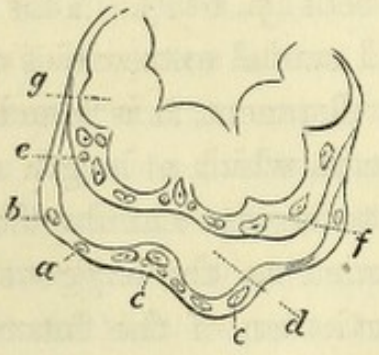
by the other set, and thus conveyed into the fœtal vessels. Not only, however, is there a passage of materials from the

*Fig.* 96.




blood of the mother into that of the fœtus, but there can be no doubt of the existence of a mutual interchange of materials between the blood of both fœtus and parent, the latter supplying the former with nutriment, and in turn abstracting from it, materials which require to be removed. Dr. Alexander Harvey's experiments (cxcix.) were very decisive on this point. The view has also received abundant support of late from Mr. Hutchinson's important observations on the communication of syphilis from the father to the mother, through the instrumentality of the fœtus (ccxiv. Dec. 1856); and still more from Mr. Savory's experimental researches (ccxxxv.) which prove quite clearly that the female parent may be directly inoculated through the fœtus. Having opened the abdomen and uterus of a

*Fig.* 97.*




* Fig. 97. Extremity of a placental villus. *a*. Lining membrane of the vascular system of the mother. *b*. External cells of the villus. *d*. Space between the maternal and fœtal portions of the villus. *e*. Internal membrane of the villus, or external membrane of the chorion. *f*. Internal cells of the villus, or cells of the chorion. *g*. Loop of umbilical vessels. After Goodsir.

pregnant bitch, Mr. Savory injected a solution of strychnia into the abdominal cavity of one fœtus, and into the thoracic cavity of another, and then replaced all the parts, every precaution being taken to prevent escape of the poison. In less than half an hour, the bitch died from tetanic spasms, the fœtuses operated on were also found dead, while the others were alive and active. The experiment, repeated on other animals with like results, leaves no doubt of the rapid and direct transmission of matter from the fœtus to the mother, through the blood of the placenta.

## DEVELOPMENT OF ORGANS.

It remains now to consider in succession the development of the several organs and systems of organs in the further progress of the embryo.

### *Development of the Vertebral Column and Cranium.*

The primitive part of the vertebral column in all the Vertebrata is the gelatinous chorda dorsalis, which consists entirely of cells (p. 649). This cord tapers to a point at the cranial and caudal extremities of the animal. In the progress of its development, it is found to become enclosed in a membranous sheath which at length acquires a fibrous structure, composed of transverse annular fibres. The chorda dorsalis is to be regarded as the azygous axis of the spinal column, and, in particular, of the future bodies of the vertebræ, although it never itself passes into the cartilaginous or osseous state, but remains enclosed as in a case within the persistent parts of the vertebral column which are developed around it. It is permanent, however, only in a few animals: in the majority it disappears at an early period.

The cartilaginous or osseous vertebræ are always first developed in pairs of lateral elements at the sides of the chorda

dorsalis. From these lateral elements are formed the bodies and the arches of the vertebræ. In some animals, as the sturgeon, however, the lateral elements of the vertebræ undergo no further development, and it is here that the chorda dorsalis is persistent through life. In the myxinoid fishes the spinal column presents no vertebral segments, and there exists merely the chorda dorsalis with the fibrous layer surrounding its sheath, which is the layer in which the skeleton originates. This fibrous layer also forms superiorly the membranous covering of the vertebral canal.

In reptiles, birds, and mammals, the mode in which the vertebræ are formed around the chorda dorsalis seems to be different. The peculiarity of this type is, at all events, distinct in the class of birds. Here the vertebræ, in that part of the spinal column which belongs to the trunk, are developed from a single pair of elementary parts. When the formation of these parts from the blastema commences, there appears at each side of the chorda dorsalis a series of quadrangular figures, the rudiments of the future vertebræ. (Fig. 84, p. 650). These gradually increase in number and size, so as to surround the chorda both above and below, sending out, at the same time, superiorly, processes to form the arches destined to enclose the spinal cord. In this primitive condition the body and arches of each vertebra are formed by one piece on each side. At a certain period, these two primary elements, which have become cartilaginous, unite inferiorly by a suture. The chorda is now enclosed in a case, formed by the bodies of the vertebræ, but it gradually wastes and disappears. Before the disappearance of the chorda, the ossification of the bodies and arches of the vertebræ begins at distinct points.

The ossification of the body is first observed at the point where the two primitive elements of the vertebræ have united inferiorly. Those vertebræ which do not bear ribs, such as the cervical vertebræ, have generally an additional centre of ossification in the transverse process, which is to be regarded as an abortive rudiment of a rib. In the fœtal bird, these

additional ossified portions exist in all the cervical vertebræ, and gradually become so much developed in the lower part of the cervical region as to form the upper false ribs of this class of animals. The same parts exist in Mammalia and man; those of the last cervical vertebræ are the most developed, and in children may, for a considerable period, be distinguished as a separate part on each side, like the root or head of a rib.

The true cranium is a prolongation of the vertebral column, and is developed at a much earlier period than the facial bones. Originally, it is formed of but one mass, a cerebral capsule, the chorda dorsalis being continued into its base, and ending there with a tapering point. This relation of the chorda dorsalis to the basis of the cranium is persistent through life in some fish, *e.g.*, the sturgeon. The first appearance of a solid support at the base of the cranium observed by Müller in fish, consists of two elongated bands of cartilage, one on the right, and the other on the left side, which are connected with the cartilaginous capsule of the auditory apparatus, and united with each other in an arched manner anteriorly beneath the anterior end of the cerebral capsule. Hence, in the cranium, as in the spinal column, there are at first developed at the sides of the chorda dorsalis two symmetrical elements, which subsequently coalesce, and may wholly enclose the chorda.

At a later period the base of the cranium contains three parts analogous to the bodies of vertebræ; the most anterior of which, in the majority of animals, is small, and its development frequently abortive, whilst in man and mammiferous animals the three are very distinct. These parts are developed by the formation of three distinct points of ossification, one behind the other, in the basilar cartilage. The three ossified portions become united by sutures, and in mammals form a rod-like body, tapering towards its anterior extremity, and giving attachment at its sides to the lateral parts of the three vertebræ.

*Development of the Face and Visceral Arches.*

Before the development of the face, the visceral cavity of the cephalic region is formed superiorly by the primitive rudimentary structure which contains the encephalon, the cerebral capsule; whilst the lower and lateral walls of that cavity are formed by the anterior "visceral arch." At this period there is no nasal cavity, and the visceral cavity of the head extends uninterruptedly from the first visceral arch to the cerebral capsule. In birds and mammiferous animals there are three *visceral arches*, and also three *visceral clefts*. The first cleft becomes converted into the external auditory passage, the tympanum, and the Eustachian tube; the second and the third are obliterated.

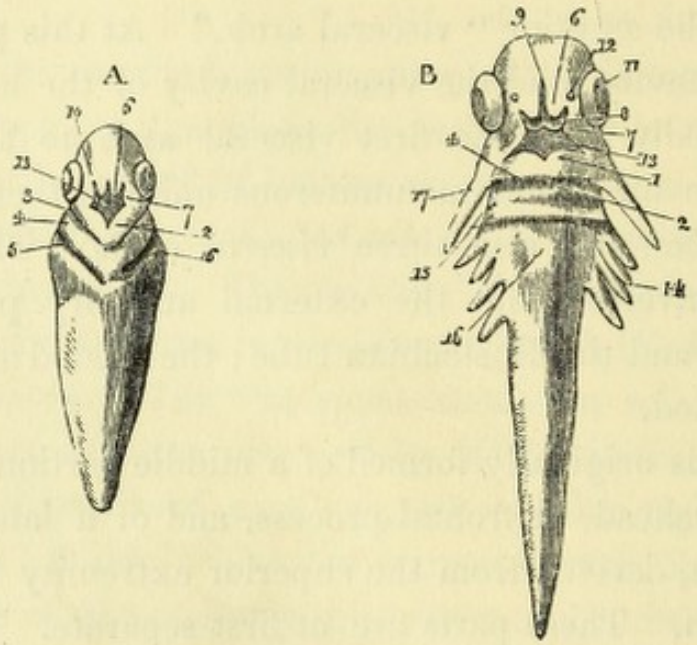
The face is originally formed of a middle portion proceeding from the forehead, or frontal process, and of a lateral portion on each side, derived from the superior extremity of the first visceral arch. These parts are at first separate. The lateral and the inferior parts, destined to form the superior and inferior maxillary apparatus, are both derived from the first visceral arch, in which an angular bend appears; the part above this bend being converted into the superior maxillary mass, and that below it into the inferior maxillary apparatus (see fig. 98). The superior maxillary mass, in its growth, approaches the frontal process, and unites with it; a cavity being left beneath that process and between the two superior maxillary masses, which becomes the nasal cavity. By the union of the superior maxillary masses (the superior maxilla and palate bone) of opposite sides beneath this cavity, the separation of the nose from the mouth by the palate is effected.

The mode of development of the face affords an explanation of the abnormal cleft palate and the congenital cleft between the upper maxillary and the intermaxillary bone, and of those congenital fissures which pass between the intermaxillary bone and upper jaw, as far upwards as the orbital cavity. Conge-

nital clefts of this kind are the results of an arrest of development occurring during the primitive conditions of the parts.

The first visceral arch, according to Reichert, produces the superior maxillary apparatus, the under jaw, and a part of the

*Fig.* 98.*




ossicula auditus, namely, the malleus and the incus. From the second visceral arch are formed the stapes of the ear, and the suspensory apparatus of the hyoid bone, *i.e.*, the styloid process of the temporal bone, the ligamentum stylo-hyoideum,

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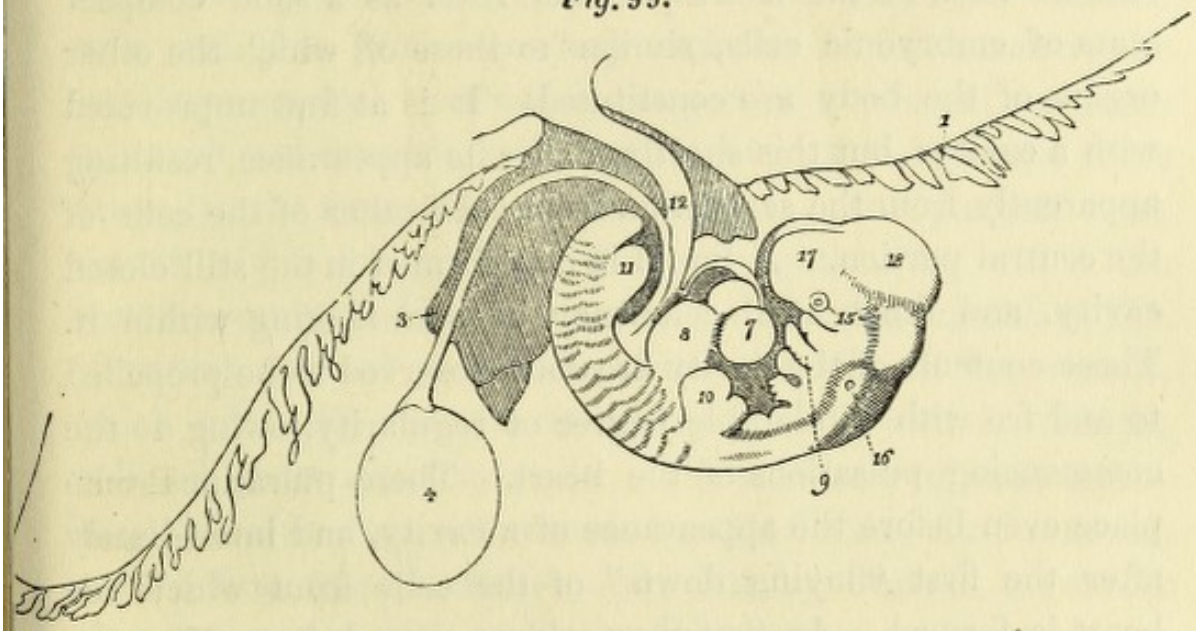
* Fig. 98. Development of the parts of the face in the embryo of Triton tæniatus. A, an embryo four lines long, magnified; B, another embryo further advanced in development. After Reichert. 1, the first visceral arch, or inferior arch of the first cephalic vertebra (incorrectly marked 2 in the figure A); 2, the second visceral arch; 3, the second visceral process; 4, the first visceral cleft; 5, the second visceral cleft; 6, the nasal or anterior frontal process; 7, rudiments of the superior maxilla; 8, rudiments of the superior intermaxillary bone; 9, the cleft between the nasal or anterior frontal processes; 10, the external nasal opening; 11, the eye; 12, the small elevation of the lachrymal bone; 13, the opening of the cephalic visceral cavity or mouth; 14, the external branchiæ; 15, the membranous branchial operculum; 16, elevated ridge pushed forward by the heart and its aortic arches.

and the smaller cornu of the os hyoides. The posterior cornua, and the body of the hyoid bone, are developed from a cartilaginous band contained in the third visceral arch.

### *Development of the Extremities.*

The extremities are developed in an uniform manner in all vertebrate animals. They appear in the form of leaf-like elevations from the parietes of the trunk (see fig. 99), at

*Fig.* 99.*




points where more or less of an arch will be produced for them within. The primitive form of the extremity is nearly the same in all Vertebrata, whether it be destined for swimming, crawling, walking, or flying. In the human fœtus the

* Fig. 99. A human embryo of the fourth week, 3½ lines in length. 2, the chorion; 3, part of the amnion; 4, umbilical vesicle with its long pedicle passing into the abdomen; 7, the heart; 8, the liver; 9, the visceral arch destined to form the lower jaw, beneath which are two other visceral arches separated by the branchial clefts; 10, rudiment of the upper extremity; 11, that of the lower extremity; 12, the umbilical cord; 15, the eye; 16, the ear; 17, the cerebral hemispheres; 18, the optic lobes or corpora quadrigemina.

fingers are at first united as if webbed for swimming; but this is to be regarded not so much as an approximation to the form of aquatic animals, as the primitive form of the hand, the individual parts of which subsequently become more completely isolated.

### *Development of the Vascular System.*

The first development of the vascular system and heart in the germinal membrane has been already alluded to. The earliest form of the heart presents itself as a solid compact mass of embryonic cells, similar to those of which the other organs of the body are constituted. It is at first unprovided with a cavity: but this shortly makes its appearance, resulting apparently from the separation from each other of the cells of the central portion. A liquid is now formed in the still closed cavity, and the central cells may be seen floating within it. These contents of the cavity are soon observed to be propelled to and fro with a tolerable degree of regularity, owing to the commencing pulsations of the heart. These pulsations take place even before the appearance of a cavity, and immediately after the first "laying down" of the cells from which the heart is formed. At first they seldom exceed from fifteen to eighteen in the minute. The fluid within the cavity of the heart shortly assumes the characters of blood. At the same time the cavity itself forms a communication with the great vessels in contact with it, and the cells of which its walls are composed are transformed into fibrous and muscular tissues, and into epithelium.

Blood-vessels appear to be developed in two ways, according to the size of the vessels. In the formation of large blood-vessels, masses of embryonic cells similar to those from which the heart and other structures of the embryo are developed, arrange themselves in the position, form and thickness of the developing vessel. Shortly the cells in the interior of a column

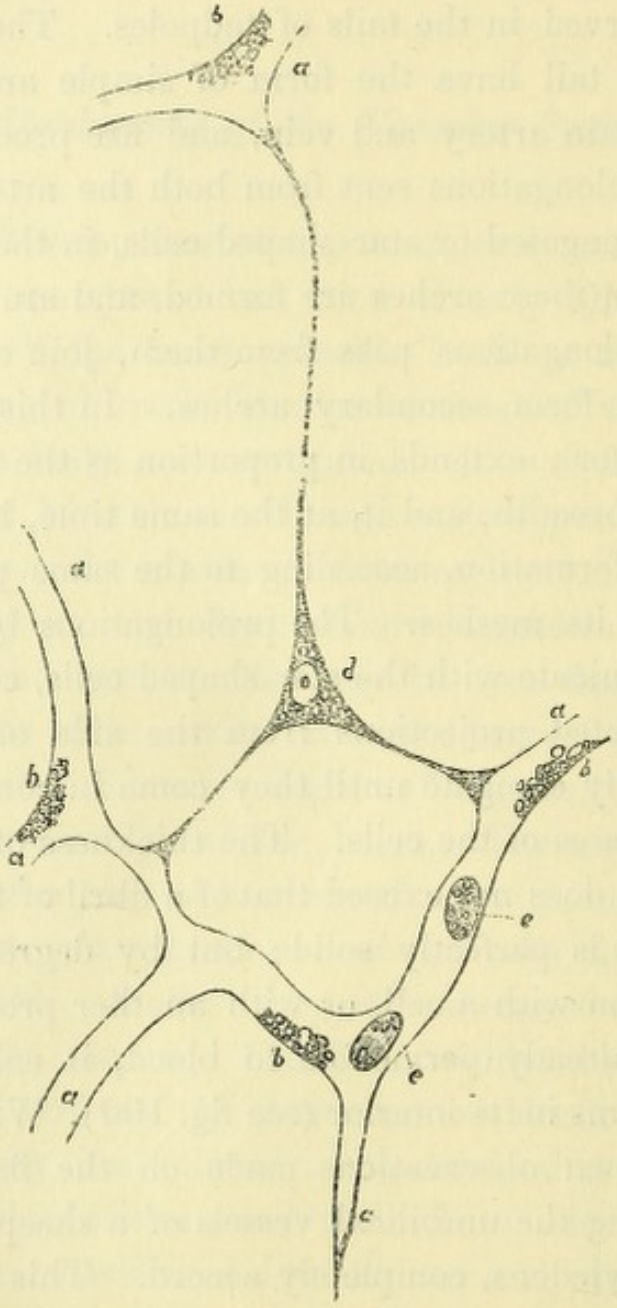
of this kind seem to be developed into blood-corpuscles, while the external layer of cells is converted into the walls of the vessel.

In the development of capillaries, another plan is pursued, This has been well illustrated by Kölliker (xxxi. August, 1846), as observed in the tails of tadpoles. The first lateral vessels of the tail have the form of simple arches, passing between the main artery and vein, and are produced by the junction of prolongations sent from both the artery and vein, with certain elongated or star-shaped cells, in the substance of the tail. When these arches are formed, and are permeable to blood, new prolongations pass from them, join other radiated cells, and thus form secondary arches. In this manner, the capillary net-work extends in proportion as the tail increases in length and breadth, and it, at the same time, becomes more dense by the formation, according to the same plan, of fresh vessels within its meshes. The prolongations by which the vessels communicate with the star-shaped cells, consist at first of narrow pointed projections from the side of the vessels, which gradually elongate until they come in contact with the radiated processes of the cells. The thickness of such a prolongation often does not exceed that of a fibril of fibrous tissue, and at first it is perfectly solid; but by degrees, especially after its junction with a cell, or with another prolongation, or with a vessel already permeable to blood, it enlarges and a cavity then forms in its interior (see fig. 100). With Kölliker's account, our own observations made on the fine gelatinous tissue conveying the umbilical vessels of a sheep's embryo to the uterine cotyledons, completely accord. This tissue is well calculated to illustrate the various steps in the development of blood-vessels from elongating and branching cells (see clxxi. p. 104).

About the time that the heart at its lowest extremity receives the venous trunks, and at its upper extremity divides into the arterial trunks or aortic arches, it becomes curved from a straight into a horse-shoe form, and shortly divides into three

cavities (fig. 101). Of these three cavities, which are developed in all Vertebrata, the most posterior is the simple auricle; the middle one the simple ventricle; and the most anterior the

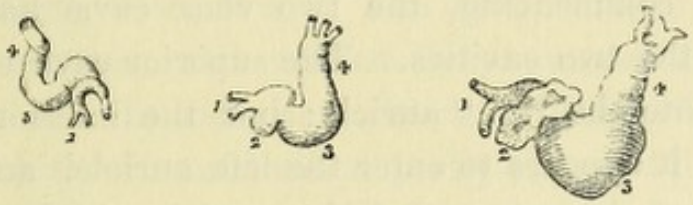
*Fig.* 100.*




* Fig. 100. Capillary blood-vessels of the tail of a young larval frog Magnified 350 times. After Kölliker. *a*. Capillaries permeable to blood; *b*, fat granules attached to the walls of the vessels, and concealing the nuclei; *c*, hollow prolongation of a capillary, ending in a point; *d*, a branching cell with nucleus and fat-granules; it communicates by three branches with prolongations of capillaries already formed; *e*, blood-corpuscles still containing granules of fat.

bulbus arteriosus. These three parts of the heart contract in succession. The auricle and the bulbus arteriosus at this period lie at the extremities of the horse-shoe. The bulging out of the middle portion inferiorly gives the first indication of the future form of the ventricle. (See fig. 101). The great curvature of the horse-shoe by the same means becomes much

*Fig.* 96.*

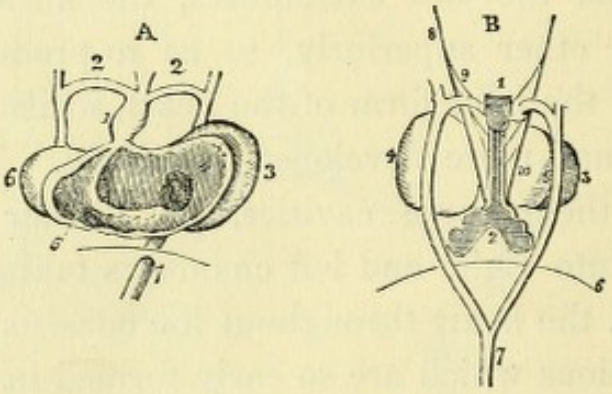


more developed than the smaller curvature between the auricle and bulbus; and the two extremities, the auricle and bulb, approach each other superiorly, so as to produce a greater resemblance to the later form of the heart, whilst the ventricle becomes more and more developed inferiorly. The heart of fishes retains these three cavities, no further division by internal septa into right and left chambers taking place. In Amphibia also, the heart throughout life consists of the three muscular divisions which are so early formed in the embryo; but the auricle is divided internally by a septum into a pulmonary and a systemic auricle. In reptiles, not merely the auricle is thus divided into two cavities, but a similar septum is more or less developed in the ventricle. In birds, mammals, and the human subject, both auricle and ventricle undergo complete division by septa; whilst, in these animals as well as in reptiles, the bulbus aortæ is not permanent, but becomes lost in the ventricles. The septum dividing the ventricle commences at the apex and extend upwards. (See fig. 102). When it is complete, a septum is developed in the

* Fig. 101. Heart of the chick at the 45th, 65th, and 85th hours of incubation. 1. The venous trunks; 2, the auricle; 3, the ventricle; 4, the bulbus arteriosus. After Dr. Allen Thomson.

bulbus aortæ, separating the roots of the proper aorta and the pulmonary artery. The septum of the auricles is developed from a semilunar fold, which extends from above downwards. In man, the septum between the ventricles, according to Meckel, begins to be formed about the fourth week, and at the end of eight weeks is complete. The septum of the auricles, in man and all animals which possess it, remains imperfect throughout fœtal life. When the partition of the auricles is first commencing, the two venæ cavæ have different relations to the two cavities. The superior cava enters, as in the adult, into the right auricle; but the inferior cava is so placed, that it appears to enter the left auricle, and the posterior part of the septum of the auricles is formed by the

*Fig.* 102.*




Eustachian valve, which extends from the point of entrance of the inferior cava. Subsequently, however, the septum, growing from above downwards, becomes directed more and more to the left of the vena cava inferior. During the entire period

* Fig. 102. Heart of a human embryo of about the fifth week. A. The heart opened on the abdominal aspect: 1, the bulbus arteriosus; 2, two aortic arches which unite posteriorly to form the aorta; 3, the auricle, 4, the opening from the auricle into the ventricle (6), which is laid open; 5, the septum rising from the lowest part of the cavity of the ventricle; 7, the vena cava inferior. B. The same heart viewed from behind: 1, the trachea; 2, the lungs; 3, the ventricle; 4, 5, the large atrium cordis or auricle; 6, the diaphragm; 7, the aorta descendens; 8, the nervus vagus; 9, its branches; 10, continuations of the nervus vagus. After Von Baer.

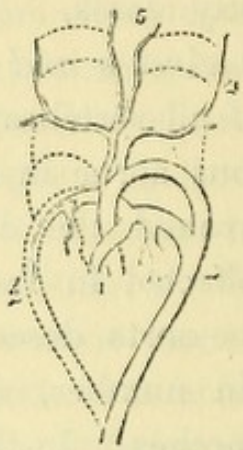
of fœtal life, there remains an opening in the septum, which the valve of the foramen ovale, developed in the third month, imperfectly closes.

*Aortic Arches and Pulmonary Vessels.*—In the early embryoes of all vertebrate animals, the blood is distributed from the bulbus aortæ in arches towards either side, and, after passing round the circumference of the visceral cavity, is again collected in front of the vertebral column into a single vessel, the aorta descendens. The aortic arches are always several in number, and at first lie in connection with the visceral arches. In those animals which breathe by branchiæ, and in which the visceral arches partly serve for the formation of the branchial apparatus, each of the aortic arches is resolved into two parallel vessels, one arterial, which comes from the heart and ramifies wholly in the branchiæ, and the other venous, which arises in the branchial laminæ, and unites with the veins of the other branchiæ in front of the aorta, to form the descending aorta. In the Amphibia, the same structure exists for a certain period; but afterwards the branchial vessels are again transformed into three aortic arches, which, when the branchial apparatus has ceased to exist, sink deeper into the thoracic cavity, and become permanent.

In Mammalia, the aortic arches are soon reduced to three, one of which is the persistent arch of the aorta, whilst the other two are the ductus arteriosi of the pulmonary artery. Of these ductus arteriosi the right also disappears; so that during the remainder of fœtal life only two aortic arches exist, one arising from the right, and the other from the left ventricle (fig. 103). The former of these gives off the arteries to the lungs, the latter the vessels to the upper parts of the body. These two arches are of equal size, and so remain until the fœtus has attained its maturity. After birth, the posterior portion of the arch, which arises from the right ventricle (the ductus arteriosus Botalli), rapidly becomes narrowed, and in the course of the first few weeks after birth, its cavity is entirely obliterated: the anterior portion becomes the trunk of the

independent arteriæ pulmonales. At the same time the closure of the foramen ovale takes place.

*Fig.* 103.*



*Veins.*—The conformation of the venous system also is at first the same in the embryoes of all vertebrate animals, and subsequently departs, in various ways, from the common primitive type. In the original condition there are two anterior venous trunks (the jugular veins), and two posterior trunks, the *cardinal veins*. One of the anterior trunks, and one of the posterior, unite on each side and form a transverse canal,—the ductus Cuvieri. The two ductus Cuvieri unite beneath the œsophagus to form a shorter main canal which enters the auricle,—at that time a simple cavity. The cardinal veins are originally formed by the caudal veins, branches from the kidneys and Wolffian bodies, and others

* Fig. 103. Plan of the transformation of the system of aortic arches into the permanent arterial trunks in mammiferous animals; after Von Baer. 1. Situation of the original single trunk which arose from the single ventricle, and which has become divided into two tubes; it gave off five pairs of aortic arches, which terminated in the two roots of the aorta (2, 2′). Those of the arches which are obliterated at a very early period are marked by dotted lines. The first arch of the right side with the root of the aorta on that side (2′) which remains longer, and forms the right ductus arteriosus, is drawn as a very narrow vessel, with a dotted line on each side. The vessels which still exist at birth are drawn of the full size. These are the first arch of the left side, constituting the ductus arteriosus Botalli, which is in greater part obliterated soon after birth, and the second arch of the left side, constituting the permanent branch of the aorta (3). The subclavian arteries (4), and the carotid arteries (5), are formed from parts of the other primitive aortic arches. After the obliteration of the left ductus arteriosus the pulmonary arteries are the only remains of the first pair of aortic arches.

from the dorsal parietes of the trunk, which are, at a later period, the intercostal and lumbar veins ; and in animals which have lower extremities, the two cardinal veins also receive the crural veins.

The omphalo-mesenteric vein, vena omphalo-meseraica, which receives the veins of the mesentery, is common to all vertebrate animals. It passes with the two ductus Cuvieri to the auricle. When the liver is formed, this vein gives branches to it, and receives from it others, the venæ hepaticæ. Between the two sets of hepatic veins the trunk of the omphalo-mesenteric becomes obliterated, and then the vena portæ is formed as an independent vessel conveying blood to the liver, while the same blood is carried out of the organ by the distinct venæ hepaticæ.

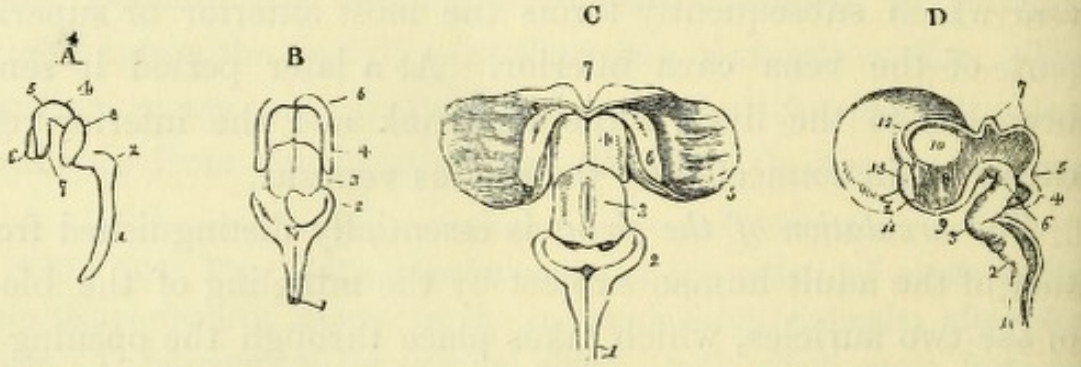
The umbilical vein originally terminates in that part of the omphalo-mesenteric vein which is about to enter the heart, and which subsequently forms the most anterior or superior part of the vena cava inferior. At a later period it sends branches to the liver, while its trunk and the inferior vena cava remain connected by the ductus venosus.

*The circulation of the fœtus* is essentially distinguished from that of the adult human subject by the mingling of the blood of the two auricles, which takes place through the opening in their septum, also by the further mixture of the blood of the two sides of the heart, which is effected through the medium of the ductus arteriosus Botalli, and further by the circumstance of part only of the blood of the right ventricle being sent to the lungs. All the blood of the body, or all the blood which the two ventricles emit, except the small quantity which the lungs receive from the right ventricle, is returned to the right auricle. The blood of the left ventricle is sent to the upper parts and also to the lower parts of the body; that of the right ventricle passes chiefly through the ductus Botalli, and supplies the lower parts of the body. All this blood returns to the right auricle. Only the fractional portion which the right ventricle sends to the lungs is collected from those organs in the left auricle.

*Development of the Nervous System.*

The mode in which the rudimentary structures of the cerebro-spinal nervous system are formed has been already stated (p. 648). The dorsal laminæ, the inner borders of which close in and form the canal of the spinal cord, seem to leave a fissure in the situation of the medulla oblongata. Between this and the most anterior extremity of the canal, several vesicular enlargements, the vesicles of the brain, are developed. (See fig. 82, p. 649). As observed by Von Baer in the chick, the cerebellum is formed early; to produce it, the laminæ, after having formed the fourth ventricle, meet again superiorly and anteriorly, and enclose a short canal leading into the vesicle of

*Fig.* 104.*




the optic lobes or corpora quadrigemina, the largest of the cerebral vesicles. The vesicle in front of that of the optic

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* Fig. 104. Early forms of the brain in the embryo, after Tiedemann. A, brain and spinal cord of an embryo of the seventh week. 1, spinal cord; 2, enlargement of the spinal cord where it makes a bend forwards; 3, cerebellum; 4, optic lobes; 5, optic thalami; 6, membranous hemispheres of the cerebrum; 7, prominence analogous to the corpus striatum. B, brain of an embryo of the ninth week. 1, spinal cord; 2, cerebellum; 3, optic lobes; 4, optic thalami, enclosing the third ventricle; 5, cerebral hemispheres. C. Brain of an embryo of the twelfth week, viewed from above, the membranous walls of the hemispheres being reflected to either side. 1, spinal cord; 2, cerebellum; 3, optic lobes; 4, optic thalami,

lobes is the vesicle of the third ventricle, the first formed, and at first the most anterior. In front of it are developed the vesicles of the cerebrum (see fig. 104, A and B). The nerves of special sense are originally hollow processes of the ventricles, the auditory nerve arising from the fourth, the optic nerve from the third, and the olfactory nerve from the lateral ventricle. The most essential parts of the organs of special sense are, therefore, in their origin, diverticula, or parts protruded from the brain. After a certain period, the vesicle of the corpora quadrigemina does not increase in size equally with the other parts, whilst the cerebral hemispheres become most rapidly developed, and extend backwards so as to cover the parts situated behind them (see fig. 104, C, D). The cerebral ganglia are produced by thickening of the walls of the primary vesicles; the corpora striata in the most anterior or cerebral vesicles, and the optic thalami in the vesicle of the third ventricle (fig 104, C).

According to Professor Retzius (cxxxv. 1846) the three lobes or portions of the cerebral hemispheres in the human embryo are developed, not at once, but at three separate periods. In the first of these periods, which extends from the second to the third month, the anterior lobes are formed; in the second period, comprised between the end of the third and the beginning of the fifth month, the middle lobes are formed; last of all, the posterior lobes are developed. The inferior horns of the lateral ventricles and the hippocampi do not appear until the second period; at this period also the optic thalami make their appearance, and after these the tubercula quadrigemina.

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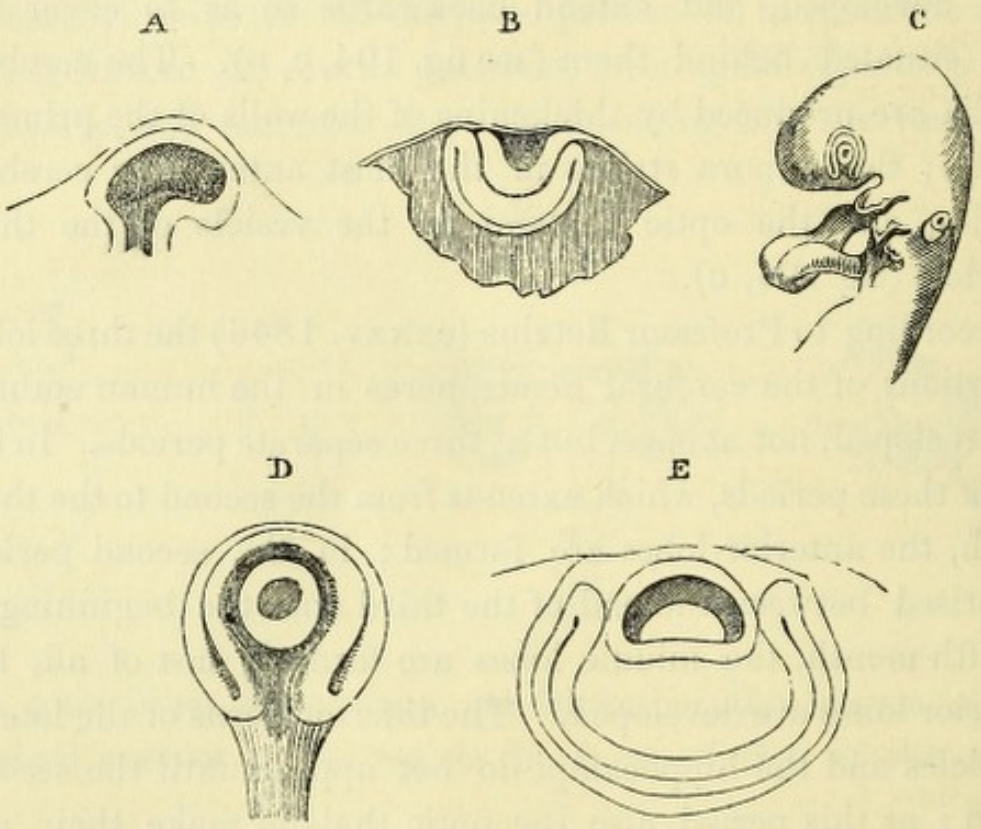
between which the third ventricle lies; 5, the walls of the hemispheres; 6, corpora striata; 7, commencement of the corpus callosum. D. Perpendicular section of the same brain. 1, spinal cord; 2, bend of the cord forwards; 3, second bend of the cord upwards; 4, cerebellum; 5, thin laminæ connecting the cerebellum with the optic lobes; 6, crura cerebri; 7, optic lobes or corpora quadrigemina; 8, cavity of the third ventricle; 9, the infundibulum; 10, optic lobe; 11, optic nerves; 12, margin of the fissure leading into the lateral ventricle; 13, corpus callosum, at this period perpendicular in its direction.

*Development of the Organs of Sense.*

The eye is in part developed as a protruded portion of the vesicle of the third ventricle of the brain, and it contains part of the membranes of the brain, namely, the fibrous and the vascular tunic. According to Huschke, the retina is originally a vesicle-like protrusion of the brain, with the cavity of which it communicates through the medium of the tubular optic nerve (fig. 105, A). The sac of the transparent media which

*Fig.* 105.*




the eye afterwards contains communicates at no period with the cavity of the brain. The capsule of the lens appears to

* Fig. 105. Development of the eye; after Huschke. A, Longitudinal section of an eye of an embryo chick of two days, enlarged thirty times. The cavities of the retina and optic nerves are seen, the whole being covered by the external tegument. C, the cephalic part of an embryo chick of the first half of the third day of incubation, magnified seven

be developed from an inverted portion of the common integuments, and consequently is at a certain period open externally (fig. 105, B). The inversion of the tegument from without, depresses the external convex surface which the vesicle of the retina has, on the second day of incubation, towards the canal of the optic nerve, and the anterior half of the vesicle is thus reflected inwards upon itself in the manner of a serous sac. The inverted layer becomes the future retina; the external layer, the membrana Jacobi.

The more recent and extended observations of Mr. H. Gray on the development of the retina and optic nerve in the chick, are at variance in some respects with the account given by Huschke. Mr. Gray was never able to see satisfactorily any doubling-in of the retina so as to form two layers, and he maintains that Jacob's membrane is not developed until a much later period (xliii. 1850, p. 189).

The iris is formed rather late, but its circle is complete at its first development. In the eye of the fœtus of Mammalia and man, the pupil is closed by a delicate membrane, the *membrana pupillaris*, the blood-vessels of which are derived from the anterior surface of the iris. From the pupillary margin of the iris there likewise extends backwards the vascular *mem-*

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times; shewing the eye with the capsule of the lens still open, surrounded by the retina, which is folded so as to consist of two layers and presents the cleft inferiorly. There are also seen the tubular looped heart, three branchial or visceral arches, and the labyrinth of the ear still open. B, is a section of the eye of the same embryo, through the middle of the lens, enlarged thirty times. The semicircular layers of membrane are seen. The most internal is the very thick capsule of the lens; the next is the true retina, the most external is Jacob's membrane. D, the eye of a chick of the third day of incubation, shewing the same parts as figure C on a larger scale. E, is the section of an eye at the fourth day of incubation of the chick. magnified thirty times. The capsule of the lens is now closed, is covered with conjunctiva, and contains a conical nucleus, the lens. The vitreous humour is developed between the capsule of the lens and the retina; external to the two layers of the retina is the sclerotic coat.

*brana capsulo-pupillaris*, which connects the margin of the capsule of the lens with the margin of the iris.

The eyelids of the human subject and mammiferous animals, like those of birds, are first developed in the form of a ring. They then extend over the globe of the eye until they meet and become firmly agglutinated to each other. But before birth, or in the Carnivora after birth, they again separate.

The *ear* likewise, according to Huschke, consists of a part developed from within, and of one formed externally. The labyrinth is developed upon the hollow protruded part of the brain which forms the auditory nerve. It appears first in the form of an elongated vesicle at the hinder part of the head of very young embryoes above the second so-named branchial cleft. From it is developed a second vesicle, the rudiment of the cochlea, the convolutions of which are then formed. The semicircular canals are produced, as diverticula of the vestibule, which terminate by again communicating with the same cavity.

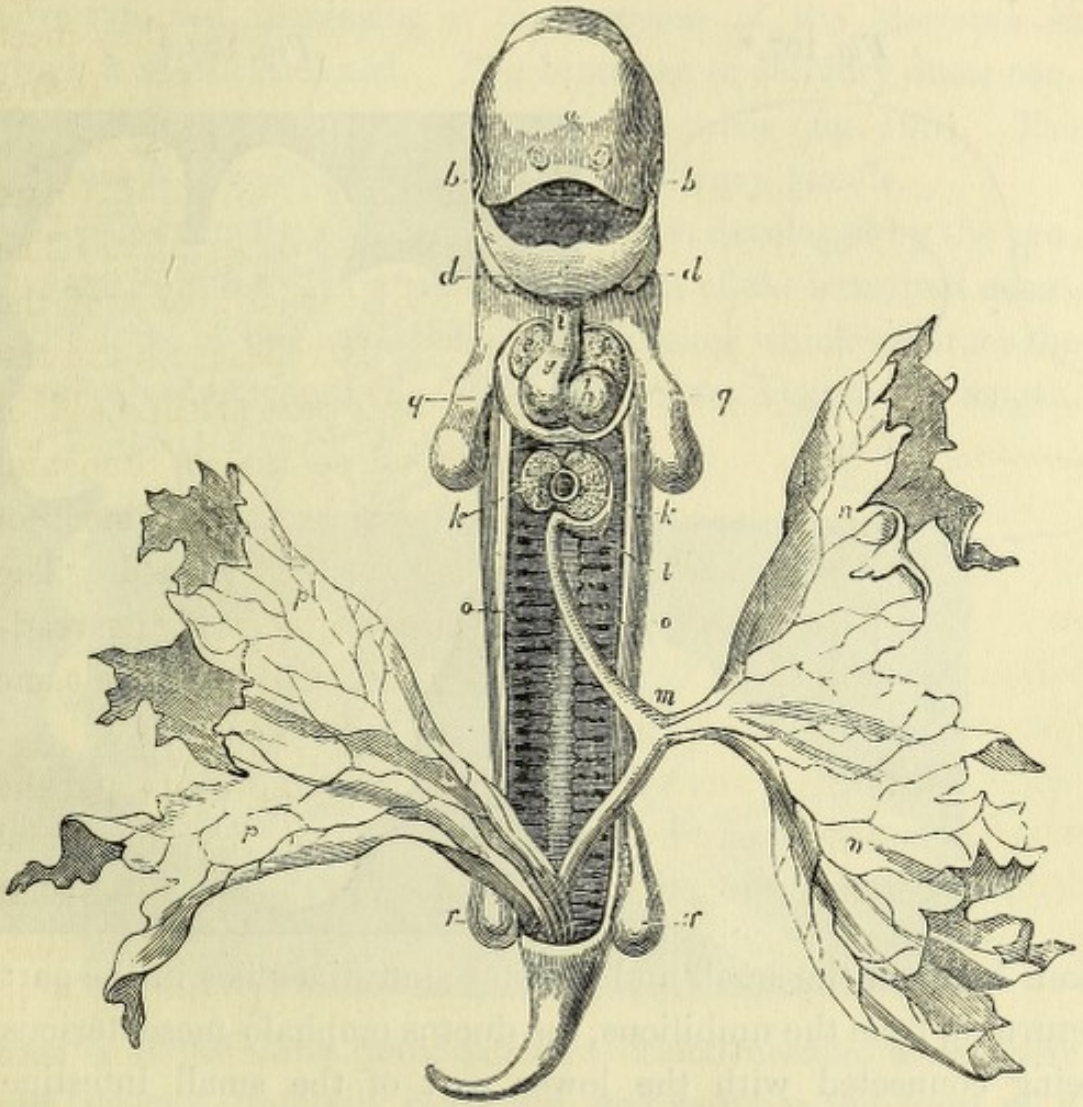
The Eustachian tube, the cavity of the tympanum, and the external auditory passage, are remains of the first branchial cleft. The membrana tympani divides the cavity of this cleft into an internal space, the tympanum, and the external meatus. The mucous membrane of the mouth, which is prolonged in the form of a diverticulum through the Eustachian tube into the tympanum, and the external cutaneous system come into relation with each other at this point, the two membranes being separated only by the proper membrane of the tympanum.

## *Development of the Alimentary Canal.*

The alimentary canal which, as already described, is a kind of diverticulum from the umbilical vessel, is at first an uniform straight tube, which gradually becomes divided into its special parts, stomach, small intestine, and large intestine

(fig. 106). The stomach originally has the same direction as the rest of the canal; its cardiac extremity being superior, its

*Fig.* 106.*




pylorus inferior. The first changes of position which the alimentary canal undergoes consists in the stomach assuming an

* Fig. 106. An embryo dog, representing the junction of the umbilical vesicle with the intestinal canal. *a*, rudimentary nostrils; *b*, rudimentary eyes; *c*, the first visceral arch; *d*, the second visceral arch; *e*, the right, *f*, the left, auricular appendage; *g*, the right, *h*, the left, ventricle, of the heart; *i*, the aorta; *k*, the liver, between the two lobes of which is perceived the divided orifice of the omphalo-mesenteric vein; *l*, the stomach; *m*, the intestine, communicating with the umbilical vesicle, *n*, *o*, the Wolffian bodies; *p*, the allantois; *q*, the upper extremities; *r*, the lower extremities. After Bischoff.

oblique direction, and in the small intestine taking a new course from the stomach towards the navel, and, after making an abrupt bend there, returning towards the middle of the body in order to make its final curve to reach the anus. The

*Fig.* 107.*

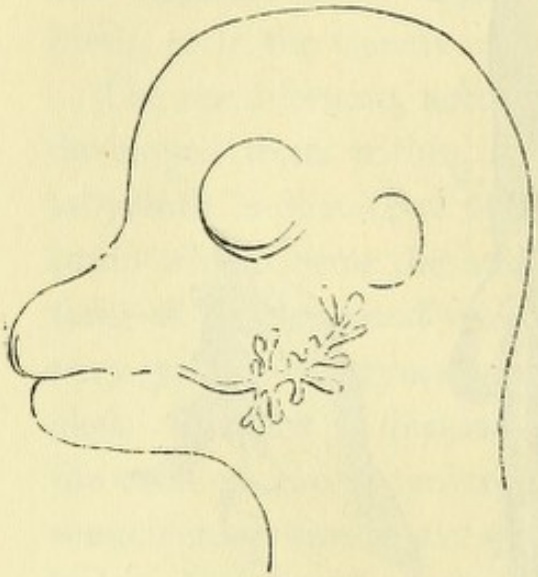
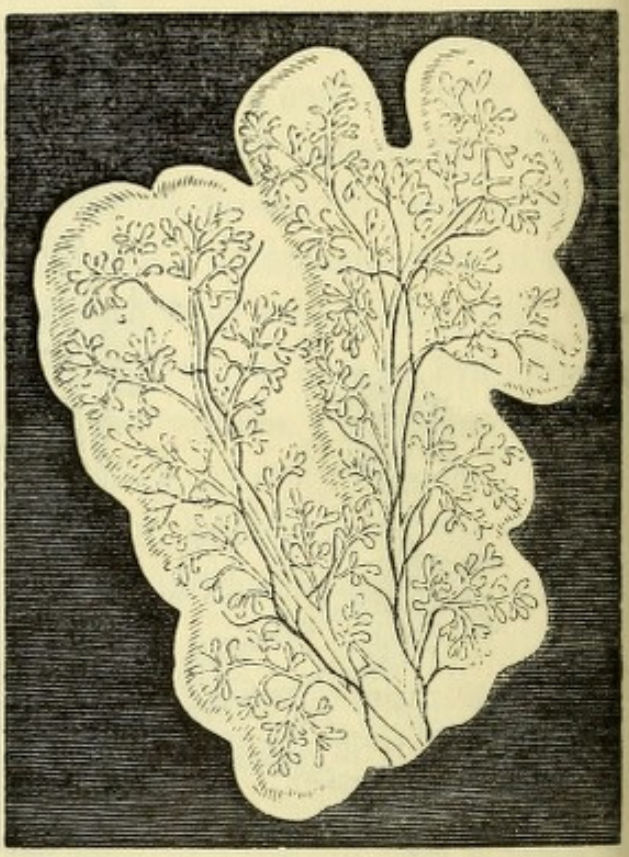


*Fig.* 108.†



limit between the small and the large intestines lies in the part returning from the umbilicus, the ductus omphalo-mesentericus being connected with the lower part of the small intestine (see plate iv. fig. 4). The part of the small intestine near the umbilicus gradually becomes elongated and convoluted (see plate iii.), and at the same time the large intestine rises so as to form its great arch round the greater part of the small intestine.

The principal glands in connection with the intestinal canal are the salivary, pancreas, and the liver. In Mammalia, each

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* Fig. 107. First appearance of parotid gland in the embryo of a sheep.

† Fig. 108. Lobules of the parotid, with the salivary ducts, in the embryo of the sheep at a more advanced stage.

salivary gland first appears as a simple canal with bud-like processes (fig. 107) lying in a gelatinous nidus or blastema, and communicating with the cavity of the mouth. As the development of the gland advances, the canal becomes more and more ramified, increasing at the expense of the blastema in which it is still enclosed. The branches or salivary ducts constitute an independent system of closed tubes (fig. 108). The pancreas is developed exactly as the salivary glands.

The liver in the embryo of the bird is developed by the protrusion, as it were, of a part of the walls of the intestinal canal, in the form of two conical hollow branches which embrace the common venous stem (fig. 109). The cones increase in length,

*Fig.* 109.*

pushing before them ramifications of blood-vessels, while their base becomes gradually narrowed, and assumes the form of a cylindrical duct. At the same time, internal ramifications are developed in the cavities of the cones, and these become united at their base, in consequence of more and more of the surrounding part of the intestinal parietes being taken up to form them, till at last the part that separated them is removed to a distance from the intestine; and the cavities, originally double,

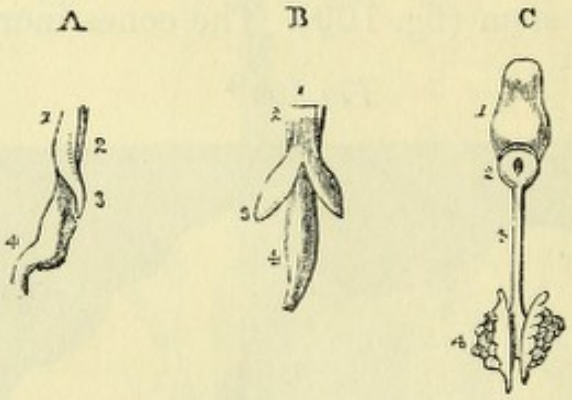
* Fig. 109. Rudiment of the liver on the intestine of a chick at the fifth day of incubation. 1, heart; 2, intestine: 3, diverticulum of the intestine in the coats of which the liver (4) is developed; 5, part of the mucous layer of the germinal membrane.

open by one mouth into the intestine. The gall-bladder is developed as a diverticulum from the hepatic duct.

*Development of the Respiratory Apparatus.*

The lungs, at their first development, appear as small tubercles, or diverticula from the abdominal surface of the œsophagus. They are united at the anterior part of their circumference; and here a pedicle is formed which becomes elongated into the trachea (see fig. 110, A, B). Soon afterwards,

*Fig.* 110.*




the lung is seen to consist of a mass of cæcal tubes issuing from the branches of the trachea. (Fig. 110, C.) The diaphragm is early developed.

*The Wolffian Bodies, Urinary Apparatus, and Sexual Organs.*

The Wolffian bodies have been already several times mentioned. They are organs peculiar to the embryonic state, and

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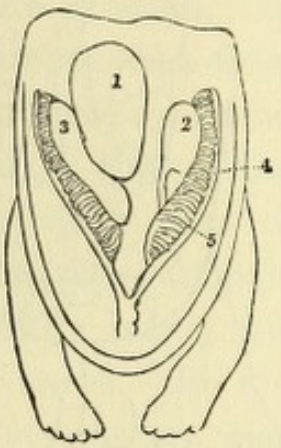
* Fig. 110 illustrates the development of the respiratory organs. A, is the œsophagus of a chick on the fourth day of incubation, with the rudiments of the trachea and the lung of the left side, viewed laterally: 1, the inferior wall of the œsophagus; 2, the upper wall of the same tube; 3, the rudimentary lung; 4, the stomach. B, is the same object seen from below, so that both lungs are visible. C, shews the tongue and respiratory organs of the embryo of a horse: 1, the tongue; 2, the larynx; 3, the trachea; 4, the lungs viewed from the upper side. After Rathke.

may be regarded as temporary, though not rudimental, kidneys; for they seem to discharge the functions of these latter organs, though they are not developed into them. They probably bear the same relation to the persistent kidneys, as the branchiæ of Amphibia do to the lungs which succeed them.

*Fig.* 111.*




In Mammalia, the Wolffian bodies are bean-shaped, and are composed of transverse cæcal canals, united by an excretory duct which leads from the lower extremity of the organ to the sinus urogenitalis or cloaca of the fœtus. (See fig. 111, 4.) The kidneys (2) and supra-renal capsules (1) are developed behind them. Their size is at first so great, that they entirely conceal the kidneys; but in proportion as the latter bodies increase in size, they grow relatively smaller, and come to be placed more inferiorly. Along the outer border of the gland runs the efferent part of the generative apparatus (5), viz., the Fallopian tube, or the vas deferens, which at first has the same conformation, and terminates by a free extremity; whilst the testicle or ovary (2) is formed independently at the internal excavated border of the organ. Subsequently the efferent tube and the testicle in the male become connected by transverse vessels, whilst in the female the extremity of the efferent tube merely acquires an open mouth. In both sexes the Wolffian bodies entirely disappear, and are not converted into any other organ. The epididymis is developed independently, that part which consists of the coni vasculosi being formed of

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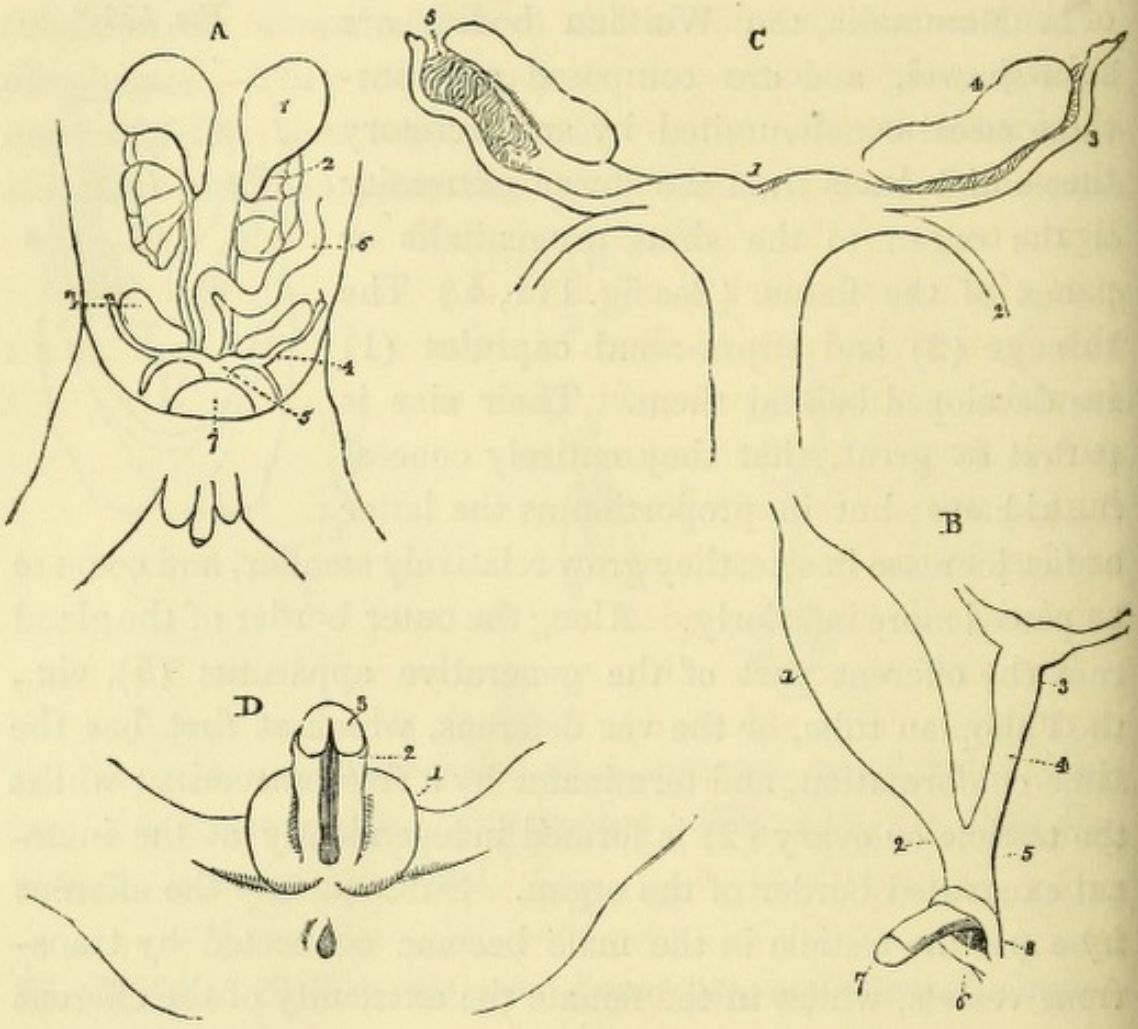
* Fig. 111. Magnified representation of the urinary and generative organs of human embryo measuring eight lines in length. 1, the supra-renal capsule of the right side, totally concealing the corresponding kidney which lies behind it; 2, kidney and ureter of the left side exposed by the removal of the supra-renal capsule; 3, testis or ovary of the right side; 4, Wolffian body; 5, Fallopian tube, or vas deferens. After Müller.

the communicating tubes which connect the efferent tube with the testis, and the rest being constituted by the convolutions of the efferent tube itself. All that part of the efferent tube or the generative apparatus which is thrown into strongly

*Fig.* 112.*




* Fig. 112. Urinary and generative organs of a human embryo measuring 3½ inches in length. A, general view of these parts; 1, suprarenal capsules; 2, kidneys; 3, ovary; 4, Fallopian tube; 5, uterus; 6, intestine; 7, the bladder. B, Bladder and generative organs of the same embryo viewed from the side: 1, the urinary bladder; 2, urethra, 3, uterus (with two cornua); 4, vagina; 5, part as yet common to the vagina and urethra; 6, common orifice of the urinary and generative organs; 7, the clitoris. C, Internal generative organs of the same embryo: 1, the uterus; 2, the round ligaments; 3, the Fallopian tubes; 4, the ovaries; 5, the remains of the Wolffian bodies. D, external generative organs of the same embryo: 1, the labia majora; 2, the nymphæ; 3, the clitoris. After Müller.

marked convolutions along the outer border of the Wolffian body, contributes to the formation of the epididymis, and from the point where the convolutions cease, a band or ligament, the gubernaculum testis Hunteri, which was developed before the convolutions of the tube were visible, and contains fibres of the cremaster muscle, passes off to the inguinal canal, and subsequently serves to guide the testis into the scrotum. In the female the tube remains free from convolutions, but from the same point as in the male, a ligament, afterwards the round ligamentum of the uterus, extends to the inguinal ring. The part of the tube which lies below the point of attachment of this ligament becomes the horn of the uterus. In those animals in which a middle portion or body of the uterus exists, this part is formed by the coalescence of the two horns. In the human uterus, the two horns gradually become shorter, and are lost in the body or fundus of the uterus which is at the same time developed. (See fig. 112, A, C).

The sinus urogenitalis, which has been mentioned, is a cavity or canal, opening externally, in which the excretory ducts of the Wolffian bodies, the ureters, and the efferent parts of the generative apparatus terminate internally. This canal is also prolonged into the urachus. Subsequently it becomes divided by a process of division extending from before backwards, or from above downwards, into a "pars urinaria" and a "pars genitalis." The former, extending towards the urachus, is converted into the urinary bladder, whilst from the latter are formed the vesiculæ seminales in the male, and the middle portion of the uterus in the female (see fig. 112, B).

The external parts of generation are at first the same in both sexes. The opening of the genito-urinary apparatus is, in both sexes, bounded by two folds of skin, whilst in front of it there is formed a penis-like body surmounted by a glans, and cleft or furrowed along its under surface. The borders of the furrow diverge posteriorly, running at the sides of the genito-urinary orifice internally to the cutaneous folds just mentioned (see fig. 112, B, D). In the female, this body becom-

ing retracted, forms the clitoris, and the margins of the furrow on its under surface are converted into the nymphæ, or labia minora, the labia majora pudendæ being constituted by the great cutaneous folds. In the male fœtus, the margins of the furrow at the under surface of the penis unite at about the fourteenth week, and form that part of the urethra which is included in the penis. The large cutaneous folds form the scrotum, and at a later period, namely, in the eighth month of development, receive the testicles, which descend into them from the abdominal cavity. Sometimes the urethra is not closed, and the deformity called hypospadia then results. The appearance of hermaphroditism may, in these cases, be increased by the testes being retained within the abdomen.

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