

**The anatomy of the central nervous organs in health and in disease / by Heinrich Obersteiner ; translated, with annotations and additions, from the third German edition, with all the alterations and corrections prepared by the author for the forthcoming fourth German edition by Alex Hill.**

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THE ANATOMY

OF THE

CENTRAL NERVOUS ORGANS



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THE ANATOMY  
OF THE  
CENTRAL NERVOUS ORGANS  
In Health and in Disease.

BY  
DR HEINRICH OBERSTEINER,  
PROFESSOR (EXT.) AT THE UNIVERSITY OF VIENNA.

SECOND EDITION.

*Translated, with Annotations and Additions, from the Third German Edition,  
with all the alterations and corrections prepared by the Author for  
the forthcoming Fourth German Edition,*

BY  
ALEX HILL, M.A., M.D., M.R.C.S.,  
MASTER OF DOWNING COLLEGE, CAMBRIDGE.

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## TRANSLATOR'S PREFACE.

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No apology is necessary for placing before the English student of neurology Professor Obersteiner's exact and impartial account of the anatomy of the central nervous system. The labour of selecting from the mass of literature, with which the subject is every year enriched, the facts of greatest importance, and the theories which harmonise most with one another, must have been immense. It would only be right that the students of all countries should be allowed to participate in the result.

In giving an English dress to Professor Obersteiner's text, the translator has attempted to transpose its forms of expression into the English mode. He has therefore taken some liberties with the phraseology without, as he hopes, in any case distorting the author's meaning; his aim being to produce a book which might pass as an English work rather than as a translation. He is greatly indebted to Professor Obersteiner for his assistance in explaining passages as to the exact force of which he was in doubt.

All additions to the text made by the translator are included in square brackets [ ]. He is also responsible for all footnotes, for the introduction of figs. 1, 2, 3, 4, 4a, 5, 7, 17a, 31, 165, 166, 167, 173, 174, 218, 219, 220, 221, 222, 223, 224, and for the Appendix. In going through Professor Obersteiner's work, care has been taken to check the references in the text, and in the footnotes to the figures, where they have been re-arranged alphabetically. Some trouble has also been spent upon the Index, into which the terms used in the German edition have been introduced, in order that the reader, who is acquainted with such terms in their German dress—and some of them have not hitherto made their appearance in English—may have the opportunity of looking up the structures which they designate in this

text-book. When doing this it seemed worth while to give the commoner synonyms and French equivalents. Not that the glossary has any pretensions to lexicographical completeness—it is merely the translator's working vocabulary.

No attempt has been made to keep step with the German edition in typography. Capital letters are used to call attention to the sections, while Italics are restricted to the names of observers quoted as authorities; personal names which are used as the appellations of structures or methods are printed in ordinary type.

The spelling of the word "neurogleia" will probably attract the attention of the reader. Neurogloea would undoubtedly be more correct, but would affect the pronunciation. In German the spelling "neuroglia" is perhaps unexceptionable, but it makes a terrible word when pronounced in the English fashion. Not only the spelling of the term but also its application is, however, open to discussion. It appears to the translator to be a useful term when applied to the connective-tissue of the central nervous system, which differs from other forms of connective-tissue in its origin from epiblast; whereas, when restricted to the "matrix," it gives an undesirable definiteness to what is, after all, a hypothetical substance.

The third German edition, from which the new English edition has been prepared, has been almost completely rewritten and greatly enlarged. Professor Obersteiner has also sent to the translator all the alterations and additions which he had prepared for the next issue in German. The book is therefore, to all intents and purposes, a fourth edition of Professor Obersteiner's classical work.

DOWNING COLLEGE LODGE,

*March* 1890.

Revised 1899.



## PREFACE TO THE FIRST GERMAN EDITION.

---

SOME decades ago our knowledge of the intimate structure of the central nervous system was still very insufficient—so insufficient, indeed, that pathology was able to make little use of it. Hence we can understand how, of the little that was known, the practitioners of the time, with very few exceptions, made use of the most striking facts only, and had to be content with an extreme poverty of data.

Since then, however, a succession of distinguished observers, supported by the improvements made in method, have, with surprising rapidity, successively thrown more light into the chaos of manifold nerve-paths and their nodal points; and therefore it had to be acknowledged in practical medicine that the brain- and spinal cord-anatomy (until now so contemptuously set aside)—despite their difficulty—are worthy of the most exhaustive consideration. Nay more, regions which seem to stand far enough away from nerve-pathology—ophthalmology, osteology, and even dermatology—have come to feel the need of a fundamental orientation of the central nervous organs.

To meet this want we possess now, especially in German, a number of most excellent anatomical text-books. But as no part of anatomy (least of all, perhaps, the anatomy of the nervous system) can be learnt from books, students and physicians seek out the laboratories where opportunity is offered them of making themselves familiar with the structure of the brain and spinal cord. Certainly, the establishment of ideally-equipped laboratories for the study of brain anatomy, such as *His* wanted at the meeting of the Berlin Association of Naturalists of 1886, will long remain *pium desiderium*. At present, teachers and students must be content with the incomplete commencements of such institutions as already exist in some of the larger universities.

Experience has now taught me what are the justifiable claims which



a beginner, who does not yet wish to become a specialist in the subject, may make upon a text-book. Especially must I assert that while, on the one hand, it is superfluous to go into incompletely established details (a course which is likely, indeed, to produce a depressing and confusing effect), yet, on the other hand, some information with regard to pathological processes should most certainly be given.

In the following pages I have tried to provide the student with a trustworthy and reliable guide, with which, in the absence of any other teacher, he may undertake the troublesome journey through the several regions of the central nervous system. Hence, I have continually introduced directions for making preparations: the numerous illustrations, although they are true to nature (with the exception of those which are purely diagrammatic), are only meant to facilitate the study of original preparations—not to replace them.

Any one who has the opportunity of visiting a laboratory with a good collection of ready-made preparations can with advantage use these, and so save himself much expenditure of time and patience in making a set of sections for himself. When, however, circumstances allow, working with the knife not only gives the dexterity necessary for undertaking independent investigations, but anatomical relations imprint themselves much more firmly upon the memory when one makes the sections for oneself, and, in especial, one obtains a clearer view of the situation of the several elements relatively to one another.

Good drawings and cleverly executed models facilitate the comprehension of difficult anatomical relations. With regard to models, however, it must be said that as yet we do not possess any that are completely satisfactory. Of the very artistic, but also very expensive, model of Aeby, *His* says, most truly, that although when we have it before us it seems very clear and transparent, it does not stand the test so soon as the eyes are removed from it.

The work under discussion, therefore, differs in many respects from existing text-books of brain-anatomy.

First, as to the manner in which the material is presented, the strictly didactic standpoint is maintained; whether the student makes preparations for himself or not, he can follow the route prescribed for him in the book. The more detailed histological relations are treated separately. The attempt has been made, while not overlooking any of the more important facts concerning the central nervous system, to avoid such minute details as should be left for special research.



The introduction of pathologico-anatomical observations, especially of the pathological changes in the elements, will prepare the road for the comprehension of the processes of disease in the central nervous system without its being in the least intended to work out an exhaustive pathological anatomy of these organs.

That a special value has been attributed to numerous and good illustrations has been already mentioned. In the choice of illustrations, which have been throughout executed in the xylographic establishment of *V. Eder* of Vienna in the most satisfactory way from original drawings, it is to be understood that a certain restraint had to be imposed to prevent the price of the book from becoming excessive. On this account, especially for drawings 118 to 136, the question had to be discussed whether the preparations chosen should be stained with carmine or according to Weigert's method. When I chose the former, I did so on the ground that I wished the illustrations to be true reproductions of the original preparations. Successful Weigert's-preparations from the adult are hardly to be made sufficiently instructive with low magnification; whereas preparations from the embryo were to be avoided on account of the difficulty which the student would find in getting the material.

I suppose I need not point out that the presentation of the material rests throughout upon autoptic observations; when facts are stated on the ground of the observations of other authors, this is in every case noted.

The usefulness of this book is further increased by the addition of an index.

HEINRICH OBERSTEINER.

VIENNA, *October* 1887.

## PREFACE TO THE SECOND GERMAN EDITION.

---

NEARLY four years ago I submitted the following work to the public, in the hope of supplying a want which I myself had felt keenly in dealing with my own pupils.

Since then the book has been in constant use in my laboratory ; and I have thus had ample opportunity of ascertaining how far it has answered, how far fallen short of its purpose. I feel myself a debtor to every pupil who has drawn my attention to omissions, to defects or obscurities of treatment. And, on the other hand, from the criticisms it has provoked in various quarters, I have gathered many valuable hints for possible alterations. As these criticisms (with few exceptions) were animated by no fault-finding spirit, but expressed the mature opinion of kindly and competent labourers in the same field, I gladly acknowledge my debt to them also, and, in preparing the second edition of this work, have given them the consideration they deserve . . . . In this connection I desire to refer particularly to the English translation by *Dr Alex Hill* of Cambridge, which appeared last year, and to which I owe a number of valuable supplementary data.

I avail myself of this opportunity to tender my sincere thanks to *Dr Alex Hill* of Cambridge, who has translated it into English, and to *Dr K. Adelheim* of Moscow, who has translated it into Russian. I also offer my sincere thanks to *Professor Koschewnikoff*, for his kind introduction to the Russian edition.

The differences between this and the first edition are mainly differences of arrangement, tending, it is hoped, to make the contents more readily available for the use of students. Special attention has been paid to the letterpress accompanying each illustration. In every case the figure and description can now be compared without turning a



page. All references to other illustrations have been cut out, so that each figure, with its accompanying description, is complete in itself. Finally, for convenience sake, I have arranged the nomenclature of the larger plates in alphabetical order.

Although the general plan of the work remains the same, the text has been carefully and thoroughly revised and much new matter added. Important investigations undertaken since the publication of the first edition have been noted wherever it was possible, and many details have been modified in conformity with the results of my own experience. I would remind the reader that I have striven, as far as in me lay, to verify personally the views which I here advance, and that where I have been forced to depend solely on the statements of other writers I have expressly acknowledged the obligation.

The chapter on Methods of Investigation has been entirely recast and greatly amplified. The portion which treats of the determination of the weight of the brain is new. The historical and comparative methods have been discussed more fully throughout, and I have endeavoured to further the understanding of anatomical structure by reference to physiology.

The treatment of pathological anatomy demands a more detailed explanation. As I observed in the preface to the first edition, I could only touch lightly upon the morbid changes of the central nervous organs, since the subject would yield material for another large volume. Yet some acquaintance with them has become so indispensable to the study and comprehension of the normal structure that they could not be passed over without notice.

I believe that a sufficiently clear and detailed view has been given of the changes of the histological elements in disease; and the pathological anatomy of the several parts has been more fully discussed (as far as space permitted) than in the first edition. Thus, nine pages have been devoted to the pathological anatomy of the spinal cord.

References to the literature of the subject seemed a most desirable addition. Here the abundance of material forbade any attempt at an exhaustive catalogue, and I have been obliged to name only the most important works of older date, and to include hardly any modern works except such as are mentioned in the text. With these for a starting-point, however, the student should be able to find out for himself the works which bear upon any special branch of inquiry.

Some of the old illustrations have been superseded by better ones, and fresh illustrations have been added. I desire to call attention to fig. 102 (the only one which I did not draw myself), for which I have to thank the skilful pencil of one of my pupils, *Herr A. Darvas*, and to figs. 151-154. The preparations depicted in them are treated by the method of medullary-sheath staining. They seem to me to answer their purpose better than preparations stained in carmine.

The fact that these alterations have increased the bulk of the volume by more than a hundred pages is one upon which I do not congratulate myself; for the more such a work can be condensed, without losing in clearness and completeness, the better will it serve its purpose. Nevertheless, I feel the absolute necessity of these additions, to enhance its practical value and to bring it one step, at least, nearer to the goal I have set before me.

I can only hope that in its new form it may meet as friendly a welcome as greeted its first appearance.

VIENNA, *July* 1891.



## PREFACE TO THE THIRD GERMAN EDITION.

---

THE transformation effected during the past four years in the scientific view of the building up of the nervous system has been so extraordinary, the conceptions which lie at the base of our ideas on the subject of the nervous organs have undergone so radical a change, as to call for a complete remodelling of the present work. The general plan remains the same, but the whole has been carefully and thoroughly revised, and in many places no stone of the original structure remains upon another.

Though feeling it essential to take note (as far as possible) of the bewildering wealth of fresh information which has been brought to light with almost incredible rapidity of late, I have striven to avoid increasing the bulk of this work to any considerable extent, lest its length should detract from its usefulness as a text-book. It nevertheless exceeds its former limits by about three-and-a-half sheets. I have been largely guided by didactic considerations in the revision, and have gladly availed myself of the experience gained from the use of the book among my own pupils.

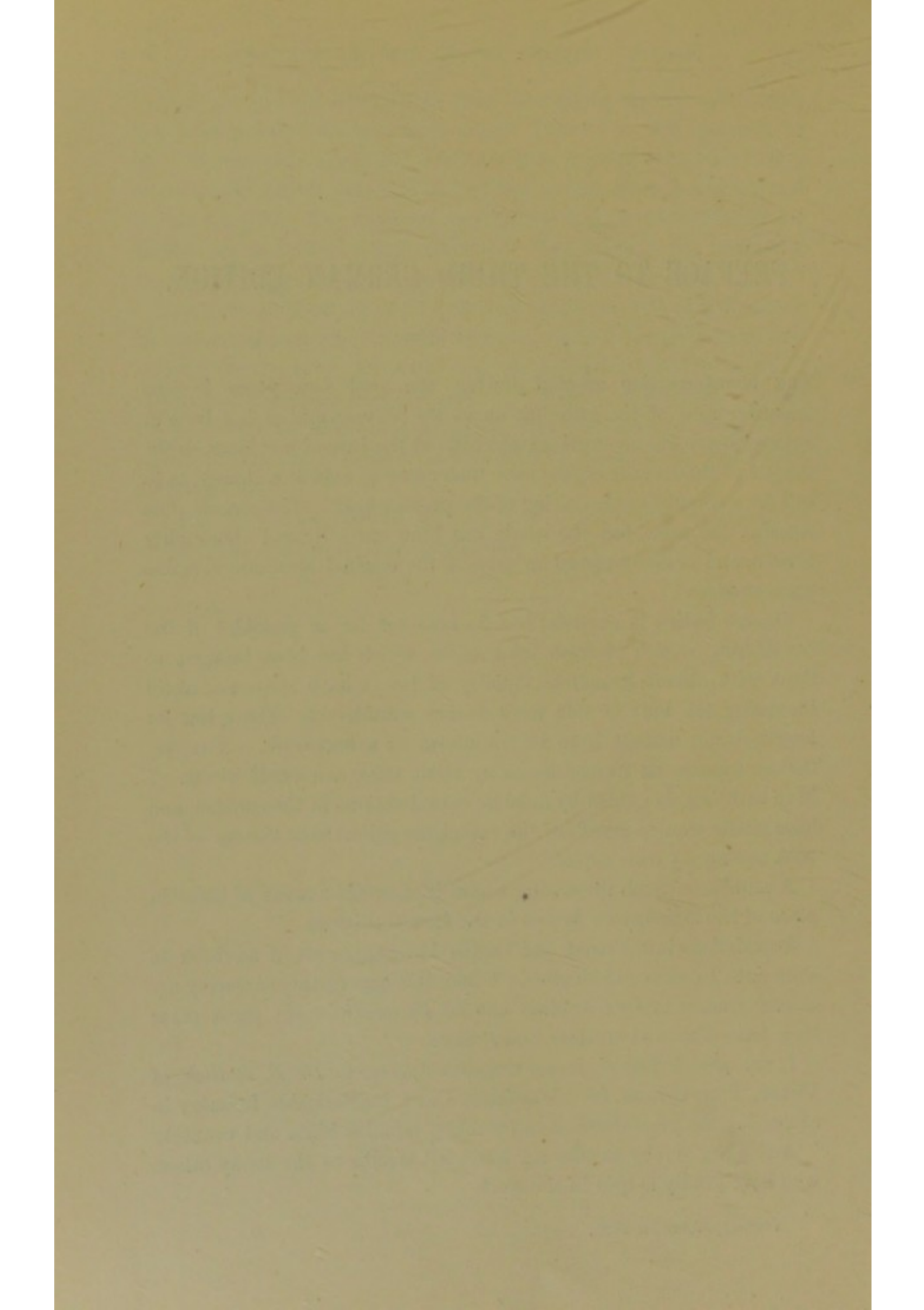
A number of fresh illustrations have been added ; many of them in place of less satisfactory figures in the former editions.

Translations into French and Italian have appeared, in addition to those into Russian and English. I take this opportunity to convey my sincere thanks to *Dr Couroënne* and *Dr Personali* for the great pains they have bestowed on these translations.

I am also indebted, in no common degree, to *Dr E. Redlich* of Vienna, Privatdocent, for his assistance and indefatigable industry in correcting the proof-sheets, and for many valuable hints and counsels.

And I beg hereby to offer my heart-felt thanks to the many others who have kindly helped in the work.

VIENNA, November 1895.





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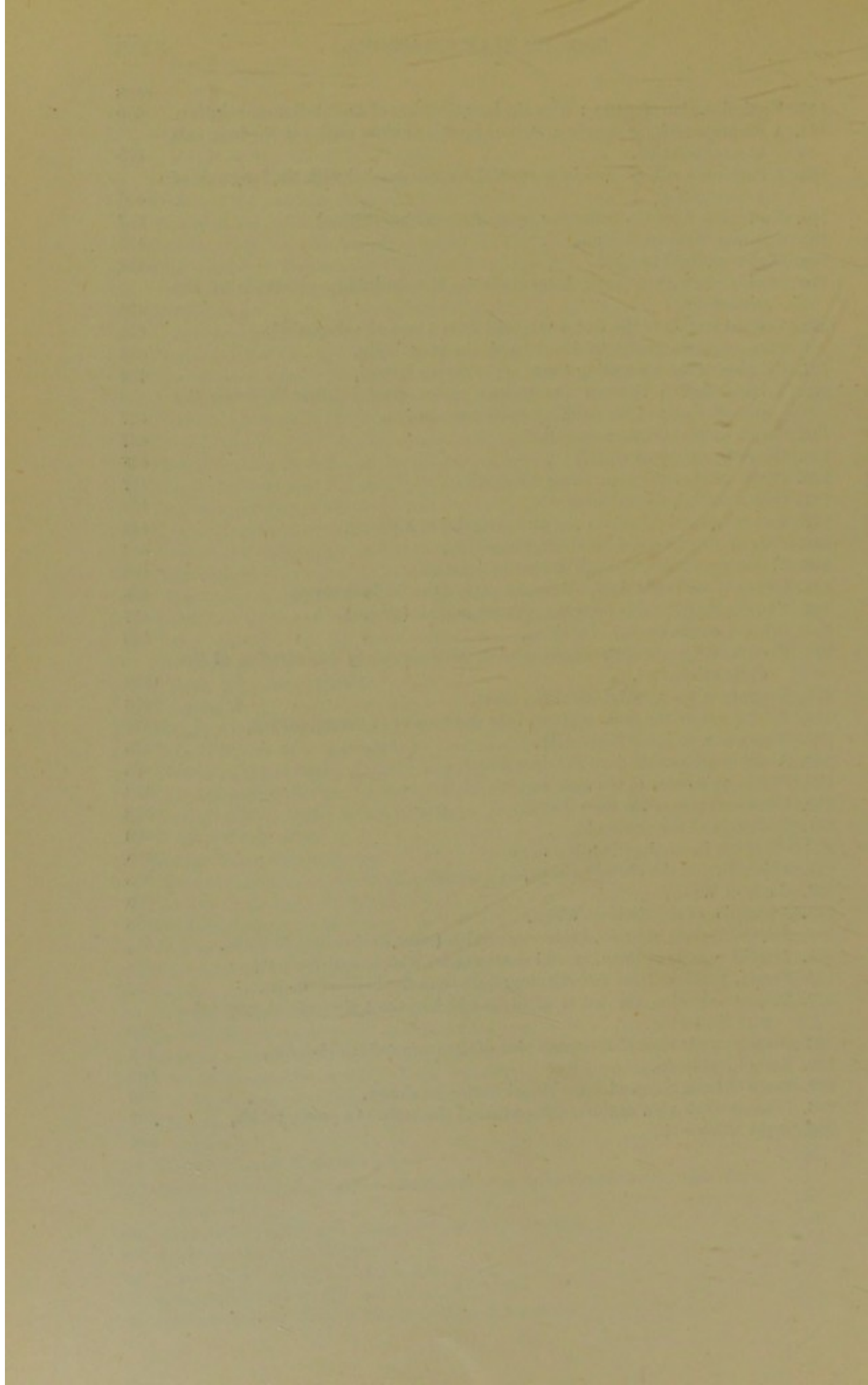
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## INTRODUCTION.

AN investigation of the complicated characters which distinguish the fine structure of the brain and spinal cord is impossible without a previous acquaintance with the more obvious features of their external configuration. Details of fine structure are often difficult to grasp, and their comprehension is facilitated by filling them into a mental outline of the organ to which they belong. Therefore, as soon as the **first section** (devoted to methods of study most in vogue) is disposed of, we shall give an account of the more obvious microscopical features of the cerebro-spinal axis, especially its external mouldings, and of such details presented by cross-sections through the brain at various levels as can be recognised without further preparation (**second section**—morphology).

Before commencing the microscopical investigation of the central nervous system by means of transparent sections, acquaintance must be made with the characters of the histological elements of which it is made up. In the **third section** an account is given of the more important nervous and non-nervous constituents of the system in health, and also of the changes to which they are subject in disease.

Next, the spinal cord is described as being relatively the simplest part of the central nervous organs (**fourth section**).

After this, we suppose (**fifth section**) that a number of cross-sections, not constituting an unbroken series, but useful for microscopical investigation, are made through the spinal cord and brain. During the preparation of such sections and their preliminary examination with an ordinary magnifying-glass, one becomes acquainted with many facts concerning their organisation, especially as one traces from section to section the changes in topographical distribution which their constituents undergo. The same routine must be followed by any one who investigates a series of sections which he has not cut for himself. He ought first to make a general survey of his preparations with a magnifying-glass, and try to obtain a stereoscopic picture of their more important features.

This done, we shall attempt, on the ground-work of knowledge thus obtained, to follow individual bundles, trace their divisions and connections, and determine their end-points. This is the object of the **sixth section**, which treats first of the fibre-routes in the spinal cord, and then



of the cranial nerves. Their finer relations are rendered intelligible by a study of the structure of the cerebellum and cerebrum.

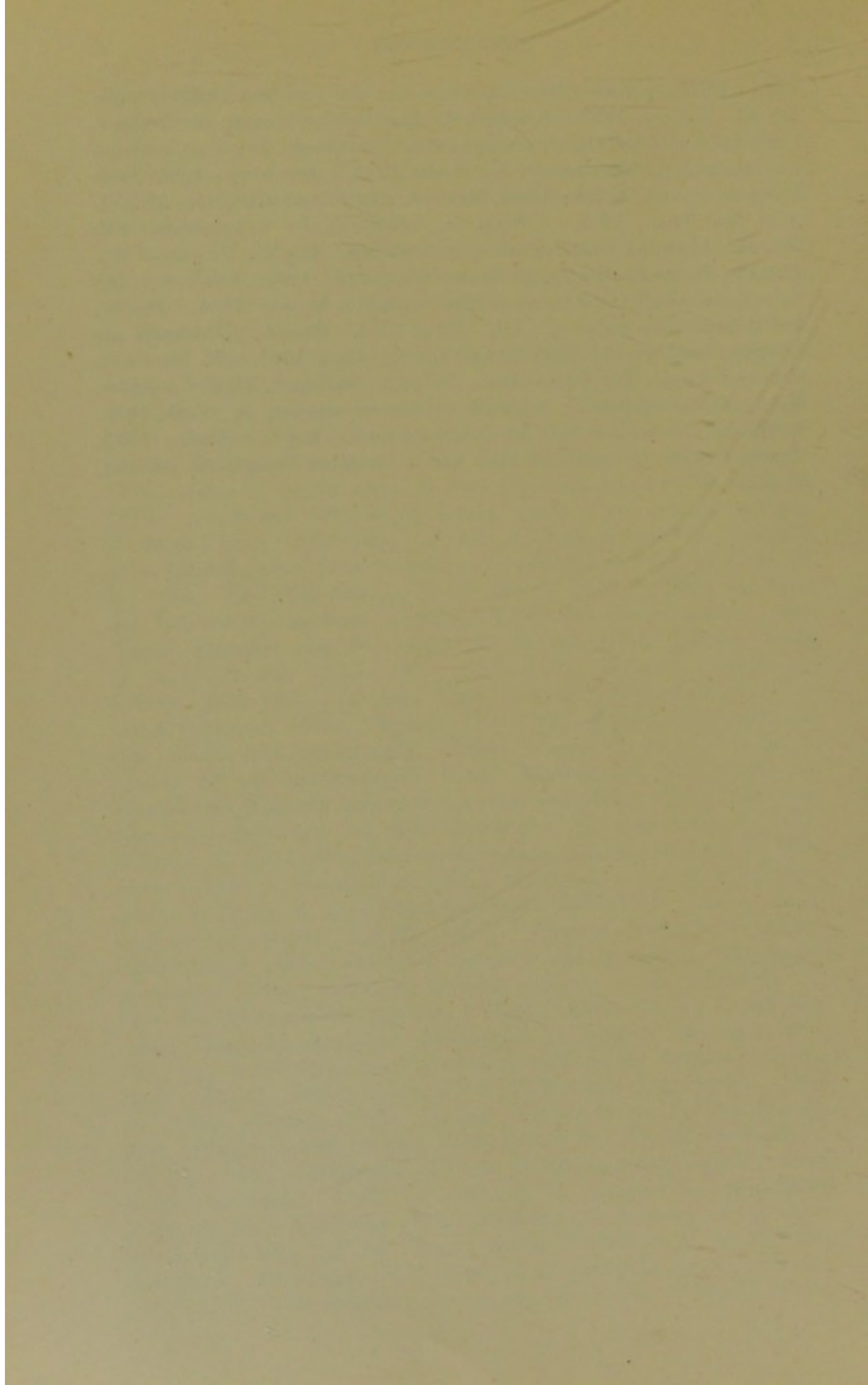
The concluding section (the **seventh**) is devoted to the meninges of the central nervous system, which stand in such close anatomical and physiological relation to the brain and cord as to deserve a special description.

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## SECTION I.—METHODS.

THE anatomical study of the central nervous system is fraught with difficulties such as are never met with in investigating other organs. The account of the structure of the brain and spinal cord about to be given, which goes somewhat further than the mere outlines of the subject, is based upon the most recent results of research in this field.

The causes of the difficulty are not far to seek. It might be anticipated that the structure of the organ to which the most various and complicated, and at the same time highest and noblest, functions are allotted, would obviously correspond in complexity to its work. It is also to be understood that this organ of relatively small size but complicated structure, made up as it is of minute nerve tracts and other parts, and composed of a delicate, soft, and destructible tissue, will hardly admit of investigation by the ordinary anatomical methods.

Such reflections alone suffice to account for the fact, that only since the introduction of special methods has this "book sealed with seven seals" been opened and its characters so difficult to read been forced to yield their meaning.

The methods in use up to the present, most of which are required for the investigation of the varying situation and connections of the elements rather than their structure, although very different in principle, yet support and complete one another.

Excluding simple anatomical inspection, we can arrange our methods in five groups, as follows:—

1. The teasing out of the fibres of a properly-prepared central nervous system.

2. The preparation of an uninterrupted series of sections through the normal fully developed organ.

3. The study of organs, the several parts of which either develop at different periods, or else have sustained retrogressive metamorphosis.

4. The comparison of homologous parts of the central nervous system in different animals.

5. The experimental observation of action, from which structure may be inferred, or the study of localised disease of the central nervous system associated with functional anomalies.

Other methods of more limited application, but none the less valuable on this account, will be detailed in their proper places.



## I. DEFIBERING.

Since the central nervous system when fresh presents a consistence which precludes the separation of fibres, it must, if this method is to be used, be subject to a preparation which, while hardening the bundles of fibres, softens the connective tissue binding them together. Such a result has not hitherto been satisfactorily obtained.

Simple hardening in alcohol to which saltpetre or hydrochloric acid (used by *Ruysch* and *Vicq d'Azyr*) or potash (*Reil*) is added has been known for a long time. Hardening in chromates with subsequent hardening in alcohol is better. External configuration is best studied after hardening in bichromate of potassium and subsequently in alcohol. *J. Stilling* places pieces of brain in Müller's fluid (see p. 8), dehydrates in spirit, and then leaves them in absolute alcohol until they attain a firm consistence. After this they are macerated in artificial wood-vinegar (200 grms. acetic acid, 800 grms. water, 20 drops of creosote). In this they remain, as a rule, for several weeks (it is impossible, however, to fix the time, for it can only be determined by experience); if the preparations become too soft they are placed for several days in crude wood-vinegar. We can with the help of forceps separate certain tracts of fibres in such pieces of brain and preserve them in Canada balsam, after treatment, in a watch-glass, with oil of cloves.

In all well-hardened spirit and chromic preparations, every artificial break in the white matter, and for the most part also in the grey masses of the brain, shows the course of fibres more or less distinctly.

It must, however, be understood that all methods of defibering, especially when the preparation contains fibres crossing one another in different directions, are apt to yield misleading results.

## 2. THE PREPARATION OF SECTION-SERIES.

To *Stilling* belongs the merit of having introduced this most useful method into brain-anatomy.

If we imagine a piece of brain cut into such a series of sections as would, if put together again, completely reproduce the original structure, we shall see that it ought to be possible, were it not for special difficulties which present themselves, to follow any transversely cut band of fibres through the whole length of the series. Although this ideal is not always attainable, it is only since the introduction of this method of making continuous series of sections that notable progress in the anatomy of the brain has been made. Further histological methods can be applied to any of the sections. But even by this method it is possible to arrive at very erroneous conclusions.

The reconstruction of an organ from the observation of a series of



transparent sections presents no little difficulty, and the conception of structure which we gain by this method needs to be checked by seeing the object itself as exposed by dissection.

When such a series is to be made, the central nervous system must first be **hardened**.

Attempts to freeze the tissue and cut it when fresh have not been successful, for the natural brain-substance suffers too much in the process, and the preparations thus obtained are unsatisfactory. The freezing method is, however, useful for tumours. We are obliged to have recourse to hardening fluids, and amongst them solutions of chromic salts stand first, and are to be preferred to simple chromic acid. Bichromate of potassium is most used. Fresh pieces of the central nervous system are placed in as large a vessel as can be had, filled with a 1 per cent. solution of this salt. The fluid is repeatedly changed for the first few days, and is rendered gradually stronger, until it is brought up to 2 or 3 per cent., at which strength the pieces are left until they are sufficiently hard. The time needed averages six to eight weeks, but depends on various circumstances, on the temperature of the room for example (it requires less time in summer than in winter); small pieces, too, take a shorter time than large ones. In an incubator, in which the temperature is maintained at from 35° to 40° C., it is possible to harden the tissue sufficiently for cutting in from eight days to a fortnight. The hardening is hastened by adding to the bichromate of potassium a little free chromic acid (20 or 30 drops of a 1 per cent. solution of chromic acid to 500 grms. of the bichromate solution). Under the influence of a constant current of electricity, emanating from the positive pole, the hardening is said to proceed with extreme rapidity, sections of the spinal cord being ready in four or five days (*Minor*). Treatment with chrome-salts should be carried out in the dark. The time required depends upon the particular part of the central nervous system under treatment. The hardening of spinal cord in chrome-salts requires especial care.

After the preparations are ready for cutting, they can still remain for some months in the chromic solution without injury; if they are to be preserved still longer, and if the use of alcohol is to be avoided, they must be transferred to a weak solution (0.5 per cent.) of the salt, in which they can be kept for years. The formation of mould is no sign that the preparations are spoilt. The addition of a little carbolic acid does not prevent the formation of fungi, but checks their growth.

Even though the pieces are thoroughly hardened in chrome-salts they can still bear the subsequent hardening in alcohol. This is accomplished usually by washing them out first for several days in water [it is not, as a rule, however, advisable to place them directly in water, but to transfer them from the solution of chromates to 25 or 30 per cent. spirit, which is changed every day until the liquor drawn off is almost colourless], and then for a like time in 50 per cent. alcohol, after which they are transferred to strong (95 per cent. or, in some cases, absolute) alcohol. To prevent precipitation it is recommended that the vessels should be kept



in the dark (*H. Virchow*). A long maceration in alcohol renders such preparations easier to cut, but destroys certain details of structure. Owing to a partial solution of the myelin by the alcohol, various spots, spaces, and so forth, often very troublesome, are artificially produced. If we desire to stain the myelin-sheath, the dehydration by absolute alcohol must be omitted. The preparations in this case are only washed in water, and are placed at once in a 95 per cent. solution of alcohol, which should be frequently changed. Since the introduction of the method of embedding in celloidin, this last hardening process has been the one most commonly used. The use of alcohol from the commencement of hardening is to be avoided, except in certain cases in which one wishes to study details in the structure of nerve-cells (*Nissl*, p. 16). Tumours, however, may be hardened in alcohol from the beginning. Where the existence of bacteria has to be proved, it is generally necessary to avoid the use of chrome-salts.

*Müller's fluid* consists of 10 parts bichromate of potassium, 5 parts sulphate of soda, and 500 parts water. Many prefer it (and with reason) to the simple solution of bichromate of potassium. Bichromate of ammonia (which is apt to make the preparation too hard), though repeatedly recommended, can well be dispensed with.

*Erlitzky's fluid* is made by mixing 5 parts bichromate of potassium, 1 part sulphate of copper, 200 parts water. It hardens more quickly than *Müller's* fluid, but sometimes produces dark precipitates in the preparation, which have already led to mistakes. Pieces of brain can generally be hardened in formalin (1 part of ordinary 40 per cent. formaldehyde to 10 of water) without detriment to the use of staining agents afterwards.

With some practice one can tell by touching, or gently pressing, a preparation, whether it has reached the proper consistence for cutting; the safest thing to do is to try it with the razor. In the case of large pieces of tissue especially, it is advisable to harden for some days previously in formalin. For this purpose ordinary formalin should be diluted with from ten to forty times its own amount of water (4-1 per cent. solution of formalin). It may comfort inexperienced persons to know that it sometimes happens that the preparation proves to be unfit to cut, although one cannot account for this mishap.

When it is desired to prepare very small pieces of brain or cord for cutting in a condition in which the most minute details of structure, as for example the nuclear figures, may be visible, it is necessary to take the pieces quite fresh from the living or recently-killed animal, and treat them with one of the so-called **fixing media**. *Fol's* modification of *Flemming's* fluid is the best of all the fixing media yet proposed; it consists of—

1 per cent. solution of perosmic acid, . . . . .	2 parts by vol.
1     "                   "     chromic acid, . . . . .	25     "
2     "                   "     acetic acid, . . . . .	8     "
Water, . . . . .	68     "



It does not do to be economical with this fluid. It should be changed as soon as it appears cloudy. After some hours (even up to twenty-four or more) the preparation is carefully washed until all traces of the hardening fluid are removed, and then preserved in 80 per cent. alcohol.

The preparation of sections, which need often to be of very large size, used to require a skilful steady hand and long practice; but the difficulties are now very much reduced by the introduction of the **microtome**. In many cases that designed by von Gudden, and made by Katsch of Munich, will be found the most satisfactory. By it sections can be cut under water; as of the cortex cerebrum, for example, when the nerve-cells are to be made clearly distinguishable.

At the present time, and especially since a decided preference has arisen for making sections only of such pieces as have first been soaked in celloidin or photoxylin (*vide infra*), the sledge-microtomes have come into more general use. In these the knife, fixed to a so-called sledge, which runs on rails, is passed across the preparation, the latter being lifted after each cut through a space corresponding to the required thickness of the section, by a mechanical device which forms part of the apparatus; knife and preparation alike being kept moist with alcohol dropped from a wash-bottle. We especially recommend the sledge-microtome of Reichert of Vienna, with its automatic arrangement for lifting the sections. Weigert's modification of the 'diving-microtome' of Schanze of Leipsic is admirably adapted for large preparations, as is also that made by Reichert from Pal's design, with its circular movement of the knife. These make it possible to cut sections under alcohol, although this is unnecessary when the preparations are of good consistency and moderate size. When the section is large or perishable it is best to catch it up from the knife with a piece of filter-paper. The paper should be doubled over it, so as to cover both sides, and each envelope marked with a number. A large number of sections can thus be kept in the same jar without fear of confusion. If the celloidin-soaked preparations show a tendency to tear in the cutting, the danger may be averted by painting the surface exposed by each cut with collodion or a thin solution of celloidin, and letting it harden (which it does in from one to two minutes) before cutting the next section.

[For general laboratory purposes the most convenient form of microtome is undoubtedly one which allows the tissue to be cut frozen. In some cases a piece of tissue can be frozen, cut, stained, and mounted in glycerin and water for hasty examination in the *post-mortem* room. If the tissue has been hardened in spirit it is necessary to throw a piece of suitable size and shape into water until all spirit is removed. This takes, as a rule, about an hour; but if the piece sinks (as does not usually occur with nervous tissue) this may be accepted as a sign that most of the spirit has diffused out into the water. It is then dipped in gum and placed on the freezing-plate of the microtome. If ether is used as a freezing agent a few minutes only are required to bring the tissue into a suitable condition of hardness, which means, for some tissues, the most complete freezing possible, for others, a condition of partial thaw. Nervous tissue, when frozen hard, is,



as a rule, too brittle to cut. The surface may be partially thawed by touching it with a wet camel's-hair brush. No microtome is more suitable for cutting frozen nervous tissue than Roy's; the extremely oblique position of the razor and the circular movement enable one to avoid breaking the section transversely, as is very apt to happen when a knife is driven straight forwards through the extremely friable frozen nervous tissue. The sections are lifted from the razor into salt solution with a large wet camel's-hair brush.]

Properly hardened tissues can be embedded for cutting with the sledge-microtome in pasteboard or metal boxes filled with wax and oil, or, if they are of no great depth, they may even be stuck on a piece of cork. If they are to be cut on cork they must be placed with the cork in a thick solution of gum, out of which both are lifted together into absolute alcohol in which they remain for twenty-four hours. Better still is the treatment with a thick solution of celloidin, which I give in detail below, as gum is apt to become so hard as to injure the knife.

To insure the uniform thickness of the sections, it is almost always necessary to have recourse to the method of embedding, or (more strictly speaking) soaking the preparations in celloidin or photoxylin. The solution for this purpose is made by putting small pieces of celloidin into a mixture of equal parts of sulphuric ether and absolute alcohol. The amount of celloidin must be determined by the required thickness of the solution. As celloidin dissolves very slowly (especially after it has once hardened) it is often better to use photoxylin, which is entirely dissolved after a few minutes in the same mixture.

The preparation must first be completely dehydrated in absolute alcohol (pieces of spinal cord about 1 centimeter thick, taken out of a watery solution, are placed for two or three days in common alcohol, and then for the same length of time in absolute alcohol; larger pieces require a correspondingly longer time). They are then put into a very thin solution of celloidin. In this they remain for a variable time according to thickness (three or four days for pieces of the size mentioned). Next they are transferred to a syrupy solution of celloidin, in which they remain a few days at least. After this a piece, now thoroughly saturated, is lifted with the adhering celloidin on to a cork or wooden block, to which it is made fast in the following manner. Its upper surface is painted freely with the thick celloidin or photoxylin solution, and exposed to the air for a while to dry. The preparation—its under surface being made as smooth as possible—is then laid on the cork and again coated with the solution to make it stick more firmly. It is left exposed to the air till the celloidin is almost set, and then cork and preparation together are placed in weak alcohol (70 or 80 per cent.). This is made by mixing the common 95 per cent. alcohol with water in the proportion of about 10 to 12. In twenty-four hours the celloidin will have hardened and be ready for cutting, but pieces stuck upon cork in this manner can safely be left in the weak alcohol for a longer period. If the sections cannot all be cut at one time, it is well to protect the cut surface with a coating of celloidin before putting cork and preparation back into the weak alcohol.



If the preparation has not a flat undersurface, or is of very irregular shape, the difficulty can be overcome by filling in with solid photoxylin, a material resembling gun-cotton. A solution of photoxylin is then poured over the whole thing, the dry photoxylin melts and unites with the liquid to form a firm homogeneous mass, which serves as a sufficient bed and support to the preparation.

When the preparations are very small, or hard to keep in position on the cork, it is usual to freeze the celloidin and cut out a block with the preparation in the middle of it. This can easily be fixed on the cork at any desired angle.

Photoxylin in solution is apt to alter in character, probably by taking up water from the air, and often to an extent which renders it quite unfit for use. From a liquid flowing with more or less difficulty, it turns into a gelatinous substance which does not cling to the fingers when touched. Nothing can be done with a solution in this state, and any preparation that happens to be in it must be dehydrated in alcohol and put into fresh photoxylin. The spoilt solution should be allowed to dry up completely by exposure to the air, and the photoxylin can then be used again.

The method of soaking in paraffin, excellent as it is for most kinds of tissue, is, on the whole, less suitable for the central nervous system. But there are not a few cases in which it is indispensable, as, for example, in dealing with the peripheral nerves, or in making minute and extremely thin sections. It cannot therefore be passed over without mention. Of this process, as of others, numerous modifications have been suggested; the following has the merit of simplicity.

The piece of tissue is first completely dehydrated and then put into a bottle of xylol, to which some small pieces of paraffin are added, either immediately or next day. These gradually dissolve in the xylol, and fresh pieces are added daily till the preparation is saturated with a tolerably concentrated solution of paraffin. It is then placed in melted paraffin (melting point about 50 deg.) for a period varying according to size from two hours to twenty-four hours. When the paraffin has set sufficiently hard the preparation is cut out with a convenient bed. The microtome razor, set well obliquely, and not moistened with alcohol, is then passed rapidly over it. The sections are first placed in xylol to dissolve the paraffin, and then transferred to carbol xylol and dammar varnish. If they have yet to be stained they are transferred from the xylol to alcohol and then, in some cases, to water or to the proposed staining fluid; but it is often advisable to stain the preparation whole before encasing it in the paraffin.

It is absolutely essential to the cutting of satisfactory sections that the preparation should be immovable in its bed, of whatever substance the latter be composed, and should be firmly fixed on the cork. Nor is it possible to lay too much stress upon the quality of the razor, by far the most important consideration in a microtome.

The sections are lifted from the razor with a soft camel's-hair brush or a strip of paper, and are generally placed in a shallow dish of weak alcohol.

The preparation of an uninterrupted section-series from a small piece of



tissue embedded in celloidin is much simplified by the following method, recommended by Weigert. One or more glass-plates of suitable size are carefully cleansed and covered with collodion as if for photography. Next strips of tissue-paper are cut a little broader than the sections and a little longer than the glass-plate. With these strips the sections are taken off the razor, the paper being held taut, lightly laid upon the section, and drawn off horizontally to the left. Each strip carries a single row of sections, the succeeding one being always received on the right side of the one before it. It is important to keep the section damp during the cutting, and until it is transferred to the glass-plate. This is accomplished by having near the microtome a shallow dish containing a number of layers of blotting-paper soaked in 80 per cent. alcohol, with a single sheet of tissue-paper on the top. On this the strips are laid during the cutting of each section and kept till wanted, the sections being on the upper surface and the paper close against the damp bed. If the glass-plates are of proper width two such rows of sections can be transferred to each by laying the strips, sections downwards, on the now dry collodion and gently pressing the back of the paper. The sections adhere to the collodion and the paper can be gently withdrawn. All superfluous alcohol being now removed without the sections being actually dried, a second film of collodion is quickly poured over them. As soon as this layer is dry on the surface the sections can be numbered with methyl-blue for future identification. The glass-plate is now either set aside in 80 per cent. alcohol or at once (before it is thoroughly dry) transferred to the staining fluid,—to the ordinary hæmatoxylin solution, for example, if the object is to stain the medullary sheaths. In this, especially if placed in an incubator, the collodion envelope soon becomes loose on the glass and can be detached easily. The further treatment of such a collodion-series is the same as I shall presently describe in speaking of separate sections in celloidin.

One of the main defects of this method is that the double layer of collodion interferes with the further treatment, and more particularly with the staining of the sections. To avoid this drawback we can make use of the expedient devised by *Obregia*, which has the further recommendation of requiring far less caution than the foregoing method. Make a mixture as follows:—40 cubic centimeters of a syrupy solution of barley-sugar in distilled water, 20 cubic centimeters of 95 per cent. alcohol, and 10 cubic centimeters of a syrupy solution of pure dextrine. This solution will keep for a considerable time. The glass-plate is covered with it exactly as with the collodion, and when dry can be put aside for several days without detriment. The sections are mounted on the glass as by Weigert's method, and after a few minutes' interval a solution consisting of 6 grammes of photoxylin or celloidin in 100 cubic centimeters of ether and the same amount of absolute alcohol is poured over them. The plate is next exposed in a horizontal position till the slight opacity around the sections has disappeared and the layer of photoxylin is set. It is then dipped into water to dissolve the sugar, and the film with the sections, which are free at one point, can be easily taken off it.



In examining preparations it is important to bear in mind that where nerve-fibres cross one another in different directions sets of fibres which would otherwise be invisible or dimly seen can be distinguished with extreme clearness by the use of *oblique lighting*, the plane mirror of the microscope being placed so that the ground about the preparation looks dark. This succeeds with preparations stained in the manner I shall proceed to describe, with carmine, hæmatoxylin, nigrosin, etc., but not with those made according to Weigert's method.

*Flesch*, also, has proposed the use of *coloured light*; where it is a matter of slight differences in colour in different parts of the section this artifice can be sometimes employed successfully.

Thicker sections may be left *unstained* and mounted in glycerin, when a very clear general view is obtained, especially with the medulla oblongata, the pons, etc., and in degenerated spots in the spinal cord the nerve-fibres that remain intact are very plainly distinguishable. Such preparations mounted in glycerin are best ringed round with paraffin. *Stilling* arrived at his epoch-making discoveries by means of preparations like these.

But in almost every case the object aimed at is to throw certain tissue-elements into greater prominence, and this is attained by *staining* in the wider sense of the term. Further, many staining-agents react very differently to the several tissue-elements, and thus allow us to make a clear differentiation in the preparation. To give an instance: hæmatoxylin stains the nuclei blue, leaving the rest of the tissue almost uncoloured. This is what we mean by *staining in the narrower sense of the term*.

Experiment has also shown that the use of metallic salts in solution and subsequent reduction causes the metal to be precipitated in or around certain tissue-elements rather than others. This fact lies at the root of the method of *impregnating with metals*.

[By far the most convenient method of using celloidin is to replace the alcohol in the celloidin-mass with water. Owing to the tissue-like permeability of celloidin, this is effected without perceptible alteration in form. The embedded preparation can afterwards be cut on a freezing-microtome. So simple is the procedure that it is well as a matter of routine to apply it invariably in investigations into the structure of the central nervous system. The tissue, either stained *en bloc* or left for staining after it is cut, is placed in absolute alcohol. This is replaced by a mixture of absolute alcohol *3 parts*, ether *1 part*. When this has soaked into the tissue a small piece of Shering's dry celloidin is placed in the vessel. The celloidin dissolves very slowly, and the gradually concentrating solution permeates the tissue far more thoroughly than even the weakest ready-made solution would do. Fresh pieces, or, to hasten the process, pieces of waste celloidin-jelly, are added daily until the solution flows with difficulty. It is then poured out with the tissue in its centre into a flat-bottomed glass dish. The dish is covered with a plate of smooth glass. By this arrangement a very slow evaporation is allowed, and the celloidin when set will be found to be of uniform consistency, and not prone to curl when cut. If it is important to save time, the celloidin is poured



into a paper boat which is immersed in chloroform, which sets the celloidin in a few hours without measurable alteration in bulk (*Caldwell*). When set somewhat firmly, the tissue with a convenient bed is cut out with a knife, and the block thrown into water for an hour (or if saturated with chloroform, into spirit and then into water). When all the alcohol is replaced by water, the block can be frozen and cut with a facility quite unattainable in spirit-set celloidin. There is no pleasanter material to cut than frozen celloidin. In some cases it is desirable to embed the tissue in celloidin, even before cutting into series of sections in paraffin. If this is desired, the chloroform-saturated block, or even the alcohol block, can be placed in melted paraffin.]

### STAINING.

The investigation of the constitution of the central nervous system by means of sections only reached its full development when *Gerlach* showed us how to treat the preparation with **staining agents** which react differently to the several tissue-elements. The stain which happened to be employed first was ammonia-carmin. To make the solution the best carmin which can be bought (*Carmin Naccarat*) is mixed in a beaker with ammonia into a soft pap, to which so much distilled water is added as will yield a dark black-red fluid. The solution is filtered, and exposed to the air until the surplus ammonia has evaporated. The solution improves on keeping. The fluid can always be filtered back into the bottle after use, and may be employed for years. Alcohol preparations are very quickly coloured in this solution; a few minutes only being needed. Chromic preparations take a varying time, increasing with the time the preparation has been kept; it may vary from an hour to several days, and each case must be treated on its own merits. When it is desired to accomplish the staining quickly, the watch-glass containing the preparation should be placed on a wire net over a vessel of boiling water; three to five minutes usually suffices under these circumstances. For preparations in celloidin this method of heating is apt to prove too violent; it is safer to place them in an incubator. The time required for staining depends upon the temperature. For slight magnification the sections are cut thick and slightly stained; for use with high powers, deep staining is necessary. Beautifully differentiated carmin-staining can sometimes be effected by diluting the solution very greatly and leaving the sections in it for a long time, perhaps a couple of days.

In carmin-staining the axis-cylinders, all cells non-nervous as well as nervous, the connective-tissue, and the epithelium should be bright red, the ground tissue pale pink, and the medullary-sheaths almost uncoloured; but many preparations take the colouring very slowly or fail altogether to present the proper sharp differentiation. In the latter case the fault lies either in the preparatory hardening or in the staining-agent. Good specimens of carmin have become so scarce, especially of late years, that many futile attempts are often made before a satisfactory solution is obtained.



Even the best solution is apt to become suddenly useless, generally owing to the formation of a bright red precipitate or the growth of a curious fungus in the fluid. Hoyer's dry carmine is more to be depended on; it should be used in a solution of about  $\frac{1}{2}$  per cent. A freshly prepared solution often yields excellent results, but it is more certain in its action if it has been kept for some time (weeks or months) in a warm temperature—by the side of the stove, for example. The action of carmine is strengthened by first soaking the preparations for a few minutes in a 1 per cent. solution of alum and rinsing them quickly before putting them into the colouring-fluid; but the clear differentiation is apt to suffer somewhat in the process.

Ranvier was the first to recommend picro-carmine instead of ammonia-carmine. A good (but not always trustworthy) picro-carmine for colouring the central nervous system is prepared by *Löwenthal* in the following way:—In 100 grms. water 0.05 gm. of caustic soda is dissolved, to this is added 0.4 gm. carmine; the mixture is then boiled for ten or fifteen minutes, and diluted to 200 c.c. To this fluid is added carefully just sufficient of a 1 per cent. watery solution of picric acid to redissolve the precipitate first formed. It then stands for two or three hours, when it is filtered several times through the same filter-paper. After some weeks or months the solution is apt to become dim.

Satisfactory results are often given by uranium carmine (*Schmaus'* method). 1.0 gm. sodic carminate and 0.5 gm. uranium nitrate are boiled in 100 cubic centimeters of water for half an hour and filtered.

A very good differentiation, similar to that given by carmine but of a grey-blue colour, is obtained by leaving the sections from ten to twenty minutes in a  $\frac{1}{2}$  per cent. watery solution of nigrosin (*Merk's* manufacture), or for half an hour in a  $\frac{1}{4}$  per cent. watery or alcoholic solution of English blue-black.

*Rosin's* method of staining is sometimes very useful for these as well as for many pathological preparations; it is rapid and brings out many details in a single section. For this we employ *Biondi's* mixture of three colours (acid fuchsin, methyl-orange, and methyl-green) in the proportion of 0.4 to 100 of water, and add to it 7 parts of a  $\frac{1}{2}$  per cent. solution of acid fuchsin. The sections are placed in this solution for five minutes. For celloidin preparations 1 part of a  $\frac{1}{2}$  per cent. solution of acid fuchsin is further added to every 4 of this fluid, and they remain in it for one minute only. The sections should then be washed quickly in distilled water (preferably in two saucers) until the colour ceases to come away in dense clouds (one or two minutes). They are next put into acetic acid (1 drop to 100 grms. water) for ten seconds, into distilled water for one minute, and into absolute alcohol until the violet colour ceases to come away (two to three minutes). Pure xylol: xylol balsam. This mixture is very selective in its action.

Sections stained by any of the foregoing methods, with the exception of *Rosin's*, are thoroughly washed in water until no more of the colouring matter comes away from them and placed in a shallow dish of 95 per cent.



alcohol, which is once changed, to be dehydrated. The time required for this depends entirely on the thickness of the section. Very small sections are sufficiently dehydrated in a few minutes. Nigrosin preparations remain in the alcohol until the desired clearness of differentiation has been arrived at. Absolute alcohol should not be used in dehydrating celloidin or photoxylin preparations, as it softens these substances.

After dehydration the sections must be cleared. The best medium for this purpose is carbol xylol (1 part of pure crystallised carbolic acid to 3 of xylol), introduced by Weigert. The section is lifted out of the alcohol with a scoop or piece of paper, and placed in a covered vessel of carbol xylol, where it remains till it is transparent, which generally occurs in a few seconds.

Many other clearing media are in use, such as oil of thyme, oil of bergamot, and creosote. Clove oil and cedar oil may also be employed for other than celloidin preparations.

When cleared, the section is mounted on a slide at once, the superfluous carbol xylol (or whatever the clearing medium may be) is sucked up with blotting-paper, the preparation is lightly pressed with a number of layers of the same, and a sufficient quantity of dammar varnish or Canada balsam dissolved in xylol is dropped on to it. The preparation is now ready, and can be covered with a cover-slip.

Sections enclosed between two pieces of paper are placed with their envelope in the xylol or oil. From this they are lifted with forceps on to the slide, and it is now easily possible to detach the upper paper. The other piece of paper is then seized with the forceps and turned over, so that the section comes to lie upon the glass. The second paper is then easily removed, provided the surplus oil or xylol on the preparation and the paper has been dried off with a number of layers of blotting-paper. The section is then treated with dammar varnish in the manner already described.

*Nissl's* method is well adapted for the examination of the structure of the nerve-cells in detail, and particularly for the detection of pathological changes. Pieces of the central nervous system, as fresh as can be procured, are put straight into 96 or 98 per cent. alcohol, in which they remain until fit for cutting. When hardened, a small piece is stuck on to a cork with gum and cut under alcohol. The sections, which should be made as thin as possible, are collected in a vessel of strong alcohol, and heated till bubbles begin to rise in the following mixture:—

Methylene-blue (B patent),	.	.	.	.	.	3.75
Venetian soap,	.	.	.	.	.	1.75
Distilled water,	.	.	.	.	.	1000

Differentiate in anilin-oil-alcohol (10 parts colourless and transparent anilin oil to 90 of 96 per cent. alcohol). As soon as the colour no longer comes away in dense clouds, the section is put on the slide and dried with blotting-paper. Next, oil of cajeput is dropped on it and dried away again when the section is transparent, then a little benzine, and it is finally embedded in benzine colophonium (1 : 10). Before the cover-slip is put on, the preparation



is passed through the flame of a spirit lamp to consume the benzine, and the cover-slip is pressed on the melted colophonium.

Unfortunately, the preparations that show clearly the structure and incidental changes of the cells are not permanent; in fact, they often lose some of their distinctness in a few minutes.

According to *Lenhossèk* the structure of the cells is most successfully exhibited by the following method. The tissue is placed for two days in a solution of ordinary 40 per cent. formalin diluted to half its original strength, then for another two days in absolute alcohol, and finally embedded in celloidin or, better still, in paraffin, as the sections must be very thin. The sections are put for about five minutes into a concentrated watery solution of thionin and washed quickly in distilled water. Differentiate in 1 part anilin oil to 9 parts absolute alcohol, clear in oil of cajeput. Dip the section into xylol for a moment, and mount in xylol dammar. This stain also fades in time.

Nissl's method can also be successfully applied to preparations which have been previously hardened in formalin. As a rule, an over strict adherence to the directions given by *Nissl* is not necessary; in many cases it suffices to leave the section from ten to fifteen minutes in methylene-blue, or to place it in the staining-fluid and hold it over the water-bath for one or two minutes; then to decolourise thoroughly in anilin-alcohol, dehydrate in alcohol, and clear in xylol (without carbolic acid) or oil of cajeput. Mount in dammar varnish.

Certain staining-agents have a peculiar affinity with the nuclei; these we call nuclear stains.

#### A. NUCLEAR STAINS.

Alum-hæmatoxylin is one of the best. We particularly recommend Ehrlich's solution, which has the advantage of keeping for any length of time. Take 5 grms. hæmatoxylin dissolved in 300 grms. absolute alcohol, with 300 grms. glycerin and the same amount of distilled water saturated with alum, mix the two together and add from 15 to 25 grms. acetic acid. Filter after some days. As the effectiveness of this solution goes on increasing for the first few weeks, it is advisable to dilute it at the end of that time with distilled water. It can always be filtered back into the bottle after use. Colouring occurs very quickly—in one or two minutes. The section, after it is washed, should only appear grey-blue, but all nuclei, except those of the nerve-cells, and amyloid bodies (when they occur) will be found strongly stained. All the rest of the section ought to be left almost or quite uncoloured. If the section is overstained it can in some cases be set right by weak salt solution. Preparations so treated can in most cases be afterwards stained quickly and beautifully in carmine. Many tumours, as well as normal tissues, can be stained in a 1 per cent. watery solution of eosin or Magdala red. The further treatment—dehydration, clearing, etc.—is the same as for carmine preparations.



Csokor's carmine stains nuclei well, and slightly colours the nerve-cells and axis-cylinders. 50 grms. powdered cochineal and 5 grms. alum are dissolved in 500 grms. of water, and the solution reduced to two-thirds its bulk by boiling. A few drops of carbolic acid are added to prevent the formation of moulds.

Numerous other nuclear stains are useful in their place—*e.g.*: (1) a watery solution of Bismarck-brown ( $1\frac{1}{2}$  to 300). (2) Grenacher's alum-carmine. Boil 1 to 5 grms. alum and 0.5 to 1.0 gm. carmine in 100 grms. water and filter. Further treatment as already described (*cf.* also p. 14). (3) Borax-carmine. Boil 1 to 2 grms. borax and 0.5 to 0.75 gm. carmine in 100 grms. water, and add enough acetic acid to bring it to the colour of the ammonia-carmine solution. Filter after twenty-four hours. The sections are placed in this fluid for a time varying from five minutes to half an hour. They come out diffusely stained, and must be placed immediately in hydrochloric acid alcohol (1 part hydrochloric acid to 100 parts 70 per cent. alcohol) in which they remain for a few minutes until differentiated, after which they are dehydrated and cleared.

Certain, as a rule, in operation, and very highly to be recommended, is van Gieson's method. Harden in chrome-salts, stain the sections in alum-hæmatoxylin (nuclear staining), wash them in water, and place in a mixture of about 1 part saturated watery solution of acid fuchsin to 3 parts picric acid in water (saturated). One or two minutes is usually long enough to leave them in this mixture. Wash in water, treat with alcohol, etc. Nerve-cells, axis-cylinders, and gleia-fibres turn red; medullary sheaths yellow; gleia-nuclei, vascular nuclei, epithelia, and amyloid bodies blue.

Adamkiewicz's staining in safranin may be classed under this head, though it cannot be described as nuclear staining pure and simple. The sections are placed in water weakly acidified with nitric acid. After a short time they are placed in the colouring solution (a deep Burgundy-red watery solution of safranin No. 0). Here they lie until they are over-stained, when they are washed first in spirit and then in absolute alcohol, which also is made slightly acid with nitric acid. Lastly, they are placed in clove oil until no more red colouring matter can be extracted from them, and mounted in Canada balsam. The nerve medulla is stained orange or red, the gleia nuclei violet. Degenerated parts come out very distinctly. Very beautiful and permanent preparations can be obtained by this method, but its results are by no means certain.

*Rehm* recommends the following process for staining the *nuclear structure of the nerve-cells*. Harden by Nissl's method (p. 16). Transfer the sections from the alcohol to carmine (carmine 1.0, ammonia 1.0, water 100.0), and leave them in it for about five minutes. Next place them for another five minutes at longest in about 100 parts 70 per cent. alcohol to 1 part nitric acid, then in pure alcohol. Finally put them for one minute into a 0.1 per cent. cold solution of methylene-blue. Differentiate in alcohol, thyme oil, benzine, colophonium. The sections should be pale violet, and should show clearly the red nuclear network in the nuclei of the blue nerve-cells. Another way is to harden the tissue in 10 per cent. nitric



acid and stain in alum-hæmatoxylin (followed up, in some cases, with methylene-blue).

### B. MEDULLARY-SHEATH STAINS.

Another set of methods has for its object the staining of the medullated nerve-fibres. For convenience, all such methods are classed together under the title of *medullary-sheath stains*, though not all of them, by any means, stain the whole medullary sheath. That first introduced by Weigert for staining in acid fuchsin presents many difficulties, and is now quite superseded by later methods.

1. *Weigert's Hæmatoxylin Method.*—The tissue must be hardened in chromic salts; but it can be transferred through alcohol into celloidin, although it is desirable that it should not be washed out in water. The block of tissue is fastened on to cork with celloidin and placed in neutral solution of copper acetate (made by mixing equal parts of saturated copper acetate solution and water). In this it remains in an incubator at 35° to 40° C. for one or two days. The sections are then cut and placed in alcohol, from which they are lifted into a solution of hæmatoxylin, prepared by dissolving 1 part hæmatoxylin in 10 parts absolute alcohol and 90 parts water. The solution is well boiled and filtered, but is not fit to use for one or two weeks. Addition of a few drops of a cold saturated solution of lithium carbonate to a watch-glass full of the fluid makes it fit for immediate use. The hæmatoxylin solution may be diluted with an equal volume of water. Solutions weaker than this do not stain sufficiently deep. In this solution the sections remain a longer or shorter time (from two to twenty-four hours), according to the degree of coloration required—spinal-cord requires a shorter time, brain-cortex a longer time. The sections, now quite black, are washed in water, and then placed in a decolourising solution composed of borax 2 parts, ferridcyanide of potassium 2.5 parts, distilled water 100 parts. Here the section remains until a differentiation between the nerve-fibres and grey matter is distinctly visible, the time necessary varying from a quarter of an hour to twenty-four hours. Owing to their blue-black colour the medullated fibres stand out sharply on a brown field. Often the decolourising fluid works too strongly, and it is advisable to thin it considerably in the case of embryonic tissue or peripheral nerves. The sections are then well washed and mounted in the usual way (alcohol, carbol xylol, dammar varnish). Since the sections which are cut after the tissue has been treated with copper acetate are not amenable to staining with carmine, it is frequently convenient to prepare a number of sections from the hardened tissue, and to submit only those to which it is desired to apply Weigert's method to the copper acetate. Sections do not require to stay so long in the incubator as directed for the block of tissue. The sections should be rinsed in weak alcohol before they are transferred to the hæmatoxylin. In cases in which staining of the finest fibres is not necessary, it is possible to dispense with the copper



solution. The sections can be left in the hæmatoxylin solution for twenty-four hours, and then, in some cases, placed for another two or three hours in the incubator ( $35^{\circ}$  to  $45^{\circ}$  C.).

As the essence of this method lies in the formation of a chrome-hæmatoxylin compound, it does not succeed if the chromic acid absorbed by the medullary sheaths during the hardening process has been washed out, either wholly or in part. Where this defect occurs it can be remedied to a certain extent by placing the sections in a strong solution of chromate of potash or a weak solution of chromic acid for a time, varying, according to circumstances, from two hours to twenty-four, and rinsing them quickly in very weak alcohol before transferring them to the hæmatoxylin or copper solution.

Weigert's method of medullary-sheath staining marks an enormous advance in the technique of nerve-histology. Both in its original form and in the modifications I shall proceed to discuss it is of inestimable value in studying the course of fibres in the central nervous system and in tracing the processes of development and degeneration in the medullary sheaths.

Other tissues besides the nerve-fibres are apt to be darkly stained by Weigert's method (or its several modifications). The contents of blood-vessels especially stain; in some cases the colourisation affects the corpuscles, in other cases the plasma. Sometimes this staining only affects the vessels in a defined region, as, for instance, in the deepest layer of the cortex. At times coagulation-products, stained intensely dark, are seen in these vessels, and easily mistaken, when thread-like in form, for medullated nerves.

Calcified vessels and nerve-cells also stain. Within the nerve-cells the pigment frequently assumes a darker colour. We notice that all nerve-cells have not reacted in the same way to the colouring agents; an attempt has been made, as we shall show later on, to make use of this difference for the classification of nerve-cells, the difference being supposed to be associated with a difference in function.

*Edinger*, also, has described extremely fine nerve-fibres, such as are supposed to exist in all vertebrate animals, on which Weigert's method of staining reacts in exactly the same way as on medullated nerves, although they have no envelope of medulla. Fibres similar to these, though in many cases much coarser, occur in invertebrate animals. This is a proof that the substance which takes the dark stain is not medulla in the strict sense of the word.

The following is Weigert's modification of his own method. Fix the tissue on cork and place it for twenty-four hours in a cold saturated solution of neutral copper acetate and 10 per cent. solution of double tartrate of potassium and sodium at a temperature of  $35^{\circ}$  C., and then for another twenty-four in a simple solution of copper. Rinse in water, place in 80 per cent. alcohol for an hour, and cut. The sections are placed in 1 part 10 per cent. alcoholic hæmatoxylin solution (freshly mixed) to 9 parts of a mixture of 7 c.c. of concentrated solution of lithium carbonate with 93 c.c. of distilled water. Further differentiation is unnecessary.



2. *Pal's Method*.—The most important modification of Weigert's method is that proposed by Pal, which deserves description in detail, as it gives excellent results. Its value consists in the *complete* decolourisation of the tissue between the medullated nerves and the opportunity of subsequently staining it, which is not allowed by Weigert's method. Pieces of tissue are hardened in Müller's fluid or bichromate of potassium. If this reagent has been completely washed out or if the tissue has assumed a green colour it must be put for a few hours into 0·5 per cent. chromic acid or for a longer time into a 2 to 3 per cent. solution of bichromate of potassium before proceeding further. The sections are put for twenty-four to forty-eight hours in Weigert's hæmatoxylin solution (p. 19), part of the time, if need be, in an incubator at 35° to 45° C., carefully washed in water, and placed in 0·5 part permanganate of potash to 200 distilled water. Here they remain from half a minute to five minutes (in some cases even longer). The right moment to take them out is when the grey matter is sharply marked off by the contrast of its brown colour with the blackness of the rest of the tissue. After washing in distilled water they are placed in the following solution:—

1 part pure oxalic acid,  
1 part sulphide of potassium,  
200 parts distilled water.

This fluid must be kept very well corked or the sulphurous acid will evaporate. A better way is to have ready a 1 per cent. solution of oxalic acid and a 1 per cent. solution of sulphide of potassium in separate bottles, and mix them in equal parts when wanted.

The section is placed in this fluid (which should have the strong pungent smell of sulphurous acid) for from half a minute to three minutes and shaken repeatedly, until the brown colouring has entirely disappeared and its place has been taken by a more or less deep shade of blue-grey. If this result does not follow, the reason is that the preparation has been too short a time in the permanganate of potash. The deficiency can be made good by washing it in water and returning it to the permanganate solution for a sufficient length of time.

When completely decolourised the section must be very carefully washed in distilled water. Dehydrate and clear in the usual way (alcohol, carbol xylol).

The best dye for further staining is Csokor's alum-cochineal (p. 18).

Not only are the separate nerve-fibres defined with extreme clearness by Pal's method, but we find single nerve-tracts characterised by striking variations of colour. Thus, the roots of the motor nerves in the mid-brain are rendered very conspicuous by their bright blue tint.

3. *Vassale's Modification of Weigert's Hæmatoxylin Method*.—The sections are placed in a solution of 1 part hæmatoxylin to 100 water for three to five minutes, then, after being quickly washed in distilled water, transferred for the same length of time to a saturated solution of neutral acetate of copper, again washed quickly in distilled water, and placed in Weigert's solution of ferrideyanide of potassium to be decolourised.



Most of the preparations given by this excellent method are in nearly every respect equal to those stained according to Weigert's directions, while its simplicity and the shortness of the time required for it are greatly in its favour. As by Weigert's method, on which it is based, the nerve-cells are rendered clearly distinguishable by their various shades of brown. The preparations are not liable to be spoilt by the formation of precipitates in the hæmatoxylin, and the sections are less brittle than those which have lain a long while in the hæmatoxylin solution. Very beautiful views of the medulla oblongata are obtained by this method; with the spinal cord it is less successful. Unless the treatment is carried out with extreme care the colour of the medullated fibres soon fades away.

4. Another method of medullary-sheath staining, introduced by *Lissauer*, has also the merit of rapidity. It is very useful in treating old long-hardened preparations, which give no good results by the ordinary hæmatoxylin methods. The sections are heated for a short time in a 1 per cent. solution of chromic acid, washed in alcohol, and then placed in Weigert's hæmatoxylin solution and heated again. Decolourisation by Pal's method.

5. *Kultschitzky's Modification of Medullated Nerve Staining*.—Harden the tissue for one or two months in Erlitzky's fluid, and wash it by putting it for several days in running water. Then place it in the following solution: 1 part hæmatoxylin dissolved in a little alcohol to 100 parts of 2 per cent. acetic acid. The deep staining of the nerve-fibres takes several hours (up to twenty-four). The sections are next placed in 100 cubic centimeters of saturated lithium solution to which 10 cubic centimeters of a 1 per cent. solution of ferridcyanide of potassium may be added to hasten decolourisation and give a warmer tone. Decolourisation is generally complete in two or three hours, but may take longer under some conditions. Wash thoroughly, dehydrate, etc. This is a very easy method, and the staining is generally clear and good. *J. Schaffer*, however, gives the preference to decolourisation in Weigert's borax-ferridcyanide solution.

6. *Wolter's method* (*Kaes' modification*), which is very often used for brain-cortex, is as follows:—After being hardened in the usual way the tissue is placed for two or three days in Kultschitzky's hæmatoxylin solution in the incubator at 42° to 45° C. It is then dipped in Müller's fluid, washed in water, and decolourised in Pal's differentiating fluid. The best way to do this is to lift the tissue in a strainer, as it should not be allowed to remain long in any one fluid. It should be dipped in the two alternately some six, ten, or fifteen times, and washed quickly after each dip. This method is said to preserve even the finest plexuses.

7. *Flechsig* recommends log-wood for staining rather than hæmatoxylin. To 1 part pure extract of Japanese log-wood, 10 parts absolute alcohol, and 900 parts distilled water, add 5 grms. of a saturated solution of sulphate of sodium and 5 grms. of a saturated solution of tartaric acid. Let the sections remain in this solution for eight days at a temperature of 35° C. Decolourise by Pal's method.

*Weigert's* recently published method of gleia-staining discloses, perhaps, most fully the behaviour of the neurogleia in the cortex.



Fresh pieces of cortex cerebri from the human brain, not more than  $1\frac{1}{2}$  centimeter thick, are placed to fix and macerate in a fluid made as follows:—Boil  $2\frac{1}{2}$  parts chromate of alum with 100 parts water in a closed enamelled pan. When it boils fast, turn out the flame and add first 5 parts acetic acid, and then 5 parts finely powdered neutral acetate of copper. Stir well with a glass tube until the copper salt is almost entirely dissolved.

The fluid should be changed on the second day. In eight days the pieces will be hardened; they should then be transferred to alcohol, embedded in celloidin, and cut. Next, the sections are placed for ten minutes in a one-third saturated solution of permanganate of potash, and washed by pouring water over them after the potash solution has been carefully drained off. The following reducing fluid is then poured over them:—Chromogen, 5 parts; formic acid (specific gravity 1.20), 5 parts; water, 100 parts. To 90 parts of this solution add 10 parts 10 per cent. solution of sulphide of sodium.

The sections should be left in this fluid from two to four hours, and then carefully washed and placed next day in a well-filtered 5 per cent. watery solution of chromogen.

They are then washed twice, and placed on the slide to undergo the actual process of staining. The slide is well cleaned with alcohol and the preparation laid quite flat on it, and dried with smooth blotting-paper. A little of the staining-fluid is then dropped on it. The fluid consists of saturated solution of methyl-violet in 70 or 80 per cent. alcohol, 100 parts; 5 per cent. watery solution of oxalic acid, 5 parts.

The staining is almost instantaneous. The section should be dried, and solution of biniodide of potassium (saturated solution of iodine in 5 per cent. solution of iodide of potassium) dropped upon it. After a short interval it should be dried again, and the process repeated, this time with equal parts of anilin and xylol. With this it should be thoroughly washed, and after that carefully washed again with pure xylol. Mount in Canada balsam. It is well to expose the finished preparation to diffuse daylight for some days.

In sections treated by this method the neurogleia-fibres are sharply defined in blue; the fibrin and nuclei are also blue; while the nerve-cells and larger axis-cylinders are brownish-yellow. The cell-bodies of the gleia-cells remain uncoloured. From observations on his own preparations Weigert therefore takes the view that in adult man the neurogleia-fibres do not represent processes of the gleia-cells, but are merely superficially attached to them.

*Kultschitzky's* is as follows: Harden the tissue in a mixture made by dissolving in 50 per cent. alcohol, to which a little acetic acid ( $\frac{1}{2}$  to 1 per cent.) has been added, as much bichromate of potash and sulphate of copper as it will hold in solution. (This should be done in the dark.) After remaining in this fluid for some time (two or three months, according to size) the tissue is further hardened in strong alcohol. This, too, is best done in the dark. Embed in paraffin, never in celloidin.



Staining fluid: 2 per cent. acetic acid, 100 parts; acid rubin, 0.25 part; saturated watery solution of picric acid, 100 parts. Three parts of this mixture are added to 100 parts 96 per cent. alcohol, the sections are placed in it for half an hour or more, and are then twice washed in alcohol. Carbol-xylol, varnish.

For the purpose of distinguishing the gelatiniferous connective-tissue from the neurogleia in sections treated by his own modification of Kultschitzky's method (p. 22), J. Schaffer recommends that they should be kept for a long time (days or weeks) in a very thin solution of eosin (about 2 drops of a 1 per cent. watery solution to 10 cubic centimeters of water). By this process the fibres of the neurogleia show white, the connective-tissue remaining brown. This differentiation succeeds as a rule only in the peripheral parts of the section.

## METHODS OF IMPREGNATING WITH METALS.

Of the principal methods of colouring by impregnation only a few of the chief need be mentioned.

1. *Exner's Perosmic Acid Method.*—Quite small pieces of nerve-tissue (at the outside not more than a centimeter thick) are placed in a sufficient quantity of 1 per cent. perosmic acid solution. The solution is changed at least once every two days, oftener when the pieces are large. In five to ten days the pieces are darkly coloured, but they may remain for a longer time in the solution. [Good results are often obtained in twelve to twenty-four hours; the preparations should, while in the osmic acid, be kept in the dark.] The preparation is then washed [a quarter to half an hour in running water is by no means too long to remove all traces of dissolved osmic acid and prevent subsequent precipitation on the addition of alcohol], placed for a few seconds in alcohol, embedded and cut. The sections, which must be very thin, are cleared in glycerin, lifted with adhering glycerin on to a slide, on which a drop of strong ammonia-water has previously been placed, and covered with a cover-glass after exposure to the air for a few minutes.

Even the finest medullated fibres are stained dark grey. The fault of this excellent method is that the preparations quickly degenerate and are often useless in a few days. [Permanent preparations, although with some faults incidental to the solution of the fat, are obtained by mounting the section, after the usual dehydration, in Canada balsam.] The method can only be applied to very small pieces of tissue.

An excellent method of staining medullated fibres in osmic acid was introduced by *Azoulay*. The tissue is hardened in Müller's fluid, then in alcohol, and embedded in celloidin in the usual way. The sections are washed and placed for five minutes to a quarter of an hour in a weak watery solution of osmic acid (1 to 500 or 1000), washed quickly in water and transferred to a 5 per cent. to 10 per cent. solution of tannic acid. In this they remain at a temperature of 50° C. until they have acquired the requisite depth of colour (which they do, on an average, in five minutes),



or they may be merely heated until the fluid gives off steam. They are then well washed and, in some cases, stained in carmine or eosin. Further treatment as usual.

This method is certain, simple, very rapid, and particularly useful in the examination of nerve-roots and peripheral nerves, parts which are often difficult to prepare satisfactorily with hæmatoxylin staining.

2. *Gold*.—The object of gold-staining is almost invariably to render the axis-cylinders conspicuous. Beautiful as gold preparations occasionally are, all methods of this sort must be regarded as more or less uncertain, at least in the case of the central nervous system. They are consequently little used.

3. *The Sublimate Colouring of Golgi*.—Little pieces of the central nervous system are, after thorough hardening in bichromate of potassium, placed in a 0.25 per cent. watery solution of corrosive sublimate. The fluid is renewed as often as it becomes coloured yellow, and the concentration of the solution may be raised to 0.5 or even 1 per cent. Small pieces are saturated in eight to ten days, but the longer they are left the more thoroughly are they permeated—larger pieces require a long time; and they may remain in the solution without harm for years. The pieces are now cut, and despite their very favourable consistence the sections need not be made very thin; they must be well washed, however, else after some weeks numerous acicular crystals of corrosive sublimate will be seen. Subsequent treatment as usual.

With low and moderate magnification certain nerve and connective-tissue cells as well as connective-tissue fibres appear intensely black. This colour is due to a fine crystalline precipitation in the tissue spaces [or lymph spaces] around the tissue-elements.

*Pal* has invented an improved sublimate method. It consists in treating the sections with sodic sulphide ( $\text{Na}_2\text{S}$ ), which gives more precise figures, black even with a high power. 10 grms. of caustic soda are dissolved in 1000 grms. of water; half of this is saturated with sulphuretted hydrogen, mixed with the other half and kept in a well stoppered bottle. The sections are carefully washed and lifted from the sublimate solution into this fluid, and remain there until the spots, at first white, become black. Subsequent treatment as usual.

*Flechsig* has invented a combination of the sublimate colouring of Golgi and medullary-sheath staining, which is said to give particularly beautiful figures. The tissue is impregnated with sublimate as in the former method, and the sections, after being stained in log-wood in the way already described (p. 22) and decolourised by Pal's method, are transferred to a mixture of 5 drops of double chloride of gold and potassium, with 20 cubic centimeters absolute alcohol. In this they remain until the precipitates formed by the sublimate have turned black, and the red bundles of nerves have assumed a bluish colour. They are then washed quickly in a mixture of 1 drop of 5 per cent. solution of potassium cyanide to 10 grms. distilled water. Dehydrate and clear.



Cox's method, as recommended by Ramón y Cajal, yields particularly beautiful results when applied to brain-cortex. Make a mixture of—

Potassium bichromate, 5 per cent. solution, . . . . .	20 parts
Sublimate solution, 5 per cent., . . . . .	20 „
Strong alkaline solution of simple chromate of potassium, . . . . .	16 „
Distilled water, . . . . .	30 to 40 „

Pieces of tissue (not too large) from the central nervous system are placed in this mixture for two or three months or even longer, then well washed in 90 per cent. alcohol, for half an hour at least, and afterwards mounted and treated like silver preparations. Sections so prepared allow of the subsequent employment of many other staining methods (alum-hæmatoxylin, for example).

4. *Impregnation with Silver*.—This method, introduced by Golgi long ago, and greatly modified and improved of late, has now assumed a place of the first importance. In the hands of various eminent anatomists, among whom, besides Golgi, we may name Kölliker, Lenhossék, Ramón y Cajal, Retzius, and van Gehüchten, it has yielded results which may fairly be said to inaugurate a new era in anatomical science as far as it deals with the structure of the central nervous organs.

In the case of tissue taken from the full-grown animal or human subject the so-called slow method of Golgi is generally the best. Small pieces (not more than 1 or 2 centimeters thick) are placed for twenty or thirty days in a 2 per cent. solution of bichromate of potassium to harden, and then transferred to a 0.75 per cent. solution of nitrate of silver. A piece is then fixed on a cork with gum and, after remaining for a short time in absolute alcohol, is cut into thick sections, which are dehydrated quickly, cleared in carbol-xylol, mounted on a slide, and covered with a drop of xylol dammar without a cover-glass.

The rapid method, as brought to perfection by Ramón y Cajal, is, however, more generally used, although it is not always successful when applied to the fully-developed organ. Pieces of tissue, as fresh as possible, are placed in a mixture of 1 part 1 per cent. osmic acid to 4 of 3.5 per cent. solution of bichromate of potash. In this fluid, which should be used with a liberal hand, the pieces remain from two to seven days in the dark and at a temperature of about 25° C. The particular tissue which takes the stain depends on the length of time for which the chrome-osmic solution is allowed to act. On Lenhossék's calculation a good time for the human spinal cord is, (1) for the neurogleia, two to three days; (2) for nerve-cells, three to five days; (3) for nerve-fibres, five to seven days.

At the end of this time the tissue is washed in a weak silver solution till no further precipitation takes place, and is then put into the 0.75 solution of nitrate of silver. The impregnation is at its best in from two to six days; the tissue suffers if left longer in the nitrate of silver. The pieces are lifted out and placed for fifteen to twenty minutes in 96 per cent., and for an equal length of time in absolute alcohol. Next, they are put into ether-alcohol or thin celloidin for about another quarter of an hour, and then for a little while into thick celloidin. Finally, they are fixed on cork



with thick celloidin, put into 80 per cent. alcohol, and cut as soon as its bed is set. The further treatment is the same as in the slow method, and the sections are mounted in dammar varnish without a cover-slip. *Van Gehuchten* advises the quick drying of the dammar varnish in the incubator at 40° C. It may be taken as a general rule that the time necessary for the reaction of the several agents must be determined to a great extent by the character of the tissue under treatment.

A quick method of hardening the brain tissue of adults is recommended by *Strong*. Small pieces are placed in 2 to 3 per cent. solution of lithium bichromate for one or two days. Further treatment as usual.

The method of staining by *double impregnation*, introduced by *Ramón y Cajal* and warmly recommended by *Lenhossék*, gives particularly successful results, even in such preparations as cannot easily be darkened by other methods. The tissue, previously treated by the rapid silver method in the usual way, is put back for a couple of days into the chrome-osmic solution (either that already used or a fresh mixture with a rather smaller proportion of osmic acid), and finally returned to the silver solution for a few days. In some cases this process may be repeated a third time.

Preparations which have been kept for some time in formol can be further treated by the rapid silver method (*Lenhossék*).

A peculiarity of silver impregnation is that it never stains more than a small proportion of the tissue-elements subject to it. Thus, in a group of ten nerve-cells we may find only one affected, but that one, in compensation, will be darkened in every branch, and down to its last and finest ramification. This circumstance is not without its advantages, for if all the cells were stained alike it would be impossible to trace the branches connected with any one of them through the complicated maze of fibres.

In examining silver preparations the student must bear in mind that the nitrate is very apt to form precipitates (in the periphery, for example) quite independent of the cell-protoplasm or other tissue-elements stained, and that under the microscope these precipitates present many deceptive figures which do not answer to anything in the structure of the tissue. Above all, let him beware of certain moss-like figures with fine ramifications, which appear constantly and have been interpreted and reproduced again and again as representing actual elements in the tissue. With very high magnification these moss-like figures are seen to consist of a central fibre of the thickness of a hair, with lateral excrescences, acicular, spherical and club-shaped, which are often of a totally different colour from the central mass.

Numerous other modifications of these methods have been proposed besides those we have enumerated.



### 3. THE INVESTIGATION OF THE CENTRAL NERVOUS SYSTEM IN EMBRYONIC AND PATHOLOGICAL CONDITIONS.

The methods arrange themselves in five groups:—

(a.) In the early periods of foetal life all nerve-fibres are destitute of medullary sheaths, so that to the unaided eye the central nervous system appears almost uniformly transparent, and of a red-grey colour. During further development all nerve-fibres are not surrounded simultaneously with medullary sheaths. White patches appear at different periods, owing to the successive acquisition by the nerves of their medullary sheaths, which occurs first in peripheral nerves and later in the central system; the ground-tissue remains grey. *Flechsig* was the first to show that the protection of the nerves with myelin does not take place at haphazard, but according to determined laws; hence important conclusions as to the structure and development of the system may be drawn from an observation of this process. By making use of this method of inspection it is possible to pick out and follow definite groups of fibres which later on are lost in the chaos of tracts. It is also possible by this method to distinguish in an apparently uniform nerve-tract constituents which, developing at different periods, must have separate functions, and it may be assumed that the functional activity of a nerve-fibre begins only when it is fully developed; *Bechterew* found the pyramidal tracts medullated at birth in all animals which can stand and run as soon as they are born, while in others they acquire the medullary sheaths later. The conclusion, therefore, may be safely accepted, that the fibres which first attain to a full development are the first to come into use.

This last assumption gains confirmation from what *Flechsig* has shown to be the fact, namely, that in animals prematurely born the fibres of the nervus and tractus opticus acquire the medulla very rapidly, and therefore that (in consequence of the functional activity of the visual organs) the development of the medullary sheaths takes place much earlier in them than in those which remain the full time in the uterus. The results obtained by *Ambrohn* and *Held* from the examination of the nervous system in new-born animals by polarised light point in the same direction. By the last-named method we are able to observe the successive stages of development in the medullary sheaths with greater precision than by any other.

The particular stages at which they acquire their structural completeness must be noted, even when these occur in extra-uterine life. No sufficiently exhaustive investigation of development under the latter conditions has as yet been set on foot.

*Weigert's* hæmatoxylin method with its certainty and simplicity has greatly helped in the investigation of the time of myelination of nerves.

It is sometimes taken for granted that a nerve-fibre, no matter how long (reaching, it may be, from the brain to the lumbar cord), gets its myelin-



sheath throughout its whole length at one time. This proposition is not proved, and it is well in using Flechsig's method to bear in mind the possibility of a difference in time in the acquisition of myelin by different parts of the nerve. It is also believed by many that a nerve acquires its myelin in the direction in which it subsequently conducts.

Embryonic conditions of the nervous system are particularly favourable for the investigation of the course of nerve-fibres by the method of silver impregnation, owing to the absence of medullary sheaths.

(b.) But there is another way in which embryology comes to the assistance of anatomical science in the study of brain-structure. By comparing the exterior and interior conformation of the brain at different stages of development, especially with a view to gaining a clearer understanding of the way in which the several parts build themselves up, we arrive at important disclosures concerning their anatomical value. By this method it has been discovered that the olivary bodies and the neighbouring groups of cells arise from the same morphological rudiment as the hemispheres of the cerebrum and cerebellum (*His*).

(c.) When a nerve (whether within or without the cerebro-spinal axis) is cut through, its peripheral end degenerates quickly. It is similarly the case that if a certain part of the white or grey substance of the cerebro-spinal axis is destroyed, by a tumour or hæmorrhage, for example, individual groups of fibres atrophy. The laws of this SECONDARY DEGENERATION—as this form of atrophy is called—are only partially known, although our knowledge of them has been greatly extended of late years. We suppose, without being able to advance irrefutable proof, that every nerve-fibre is nourished by the cell with which it is connected—its trophic centre. If the trophic centre is destroyed, or if the nerve-fibre is severed from it, the nerve necessarily dies. When a nerve-route in the central system is cut through, the part severed from its trophic centre degenerates, though that which remains in connection was originally said to remain intact (Waller's law). For most nerve-tracts, we cannot say for all, it is proved that degeneration progresses in the direction in which the impulses are in the habit of travelling along the fibre.

We are, unquestionably, much indebted for our present knowledge of the course of fibres in the central nervous system to the formulation of Waller's law, though the experiments of the last few years have demonstrated beyond the possibility of doubt that in its original form, as stated above, the theory is no longer tenable.

It has been proved that in most cases that part of the nerve which remains in connection with the cell degenerates also, the degeneration extending even to the cell itself; though decay is far more rapid and complete in the severed portion (*Forrel, Bergmann*). On the other hand, it may be observed that in slow degeneration of the nerve-cells of the cornu anterius (chronic poliomyelitis anterior) the anterior nerve-roots starting from these cells are sometimes found very slightly degenerated (*Oppenheim*).

The first results of any importance gained by the degeneration-method are associated with the name of *L. Türck*. With the help of secondary



degeneration we may now follow with exactitude the whole course of certain fibre-tracts and even of single nerve-fibres. By Weigert's hæmatoxylin method we can make the degenerated parts stand out sharply from the healthy tissue by the brightness of their colour.

Where the degeneration is not of very long standing, good results are given by the chrome-osmic staining of *Marchi* and *Algeri*. The tissue is hardened for a week at least in Müller's fluid (a longer time does it no harm). Thin slices (at the outside not more than half a centimeter thick) are placed directly, without washing, in a mixture of 2 parts Müller's fluid to 1 of 1 per cent. solution of perosmic acid and left in it for five to eight days, preferably at a temperature of 28° C., then washed and treated with alcohol and celloidin. The finished sections are dehydrated in alcohol, cleared in carbol-xylol, and mounted in dammar varnish without a cover-slip. Normal nerve-fibres are recognisable by their light brown colour, while the medullary sheath of degenerated fibres is marked by the appearance of numerous deep black globules of varying size. Small black dots are also found scattered about in normal nerve-tissue when freshly prepared, and in judging of such preparations care must be taken not to confound these with the larger degeneration-spots. It will be observed that many of these granules lie between the nerve-fibres, but none in the larger septa.

If the sections, taken as a whole, are somewhat dark, they may be decolourised by Pal's method (see p. 21), with permanganate of potash, and sulphurous acid.

*Marchi's* method of staining is most sensitive to degenerative changes in nerve-tissue. Very slight injuries to the skull, etc., sometimes set up serious degeneration, even in distant parts, which can be discerned only by this method (*Bikeles*). It is also the only method by which the fat-granule-cells can be made permanently visible in their position relative to the other tissue-elements in sections.

[The essential nerve-fibre, the axis-cylinder, is from origin to termination a process of a nerve-cell. The nerve-cells are brought into relation with one another by branching processes; but whether the ultimate twigs are permanently united, or whether they are merely placed in physiological continuity, as occasion requires, is a question on which opinions differ (*cf.* p. 157). Most histologists hold the latter view. The central system offers a variety of alternative routes to the afferent impulse. Wherever a long efferent fibre starts from the system, the cell of which it is a process and from which it grows out, is found to present a size proportional to that of the fibre to which it gives origin, and over the nutrition of which it permanently presides. At its distal end the fibre branches for the purpose of establishing a connection with the region towards which it grows out. No nutriment is received from this dendritic termination backwards along the fibre, but throughout its whole length the fibre depends for its vitality upon its connection with the cell from which it sprang. The nerve-fibre dies when cut off from the cell of which it is a process. From this account of



the nutrition of nerve-fibres, it will be understood that within the cerebro-spinal axis, motor (descending) fibres degenerate below the level of section; sensory (ascending) fibres degenerate above this level. The portions of the white columns, in the immediate vicinity of the grey matter, consist of fibres which connect together neighbouring regions of the plexus, and it is consequently very difficult to obtain evidence as to the direction in which they die; for the fibres which the lesion destroys are so short, that even in a section taken a little way above or below the lesion, the same situation in the axis is already occupied by other sets of fibres.

When an anterior spinal nerve-root is cut, the fibres below the section die, as shown by *Waller*. The distal portion of the root degenerates completely, as do also all the fibres which the anterior root yields to the mixed nerve. When the posterior root is cut proximally to its ganglion, all its fibres die between the section and the spinal cord; all the fibres between the section and the ganglion live. Until recently it was thought that if the posterior root is cut on the distal side of the ganglion, all the fibres between the section and the ganglion live, while all those which the section severs from the ganglion die. This has been shown by *Max Joseph* not to be quite correct; the greater number of the fibres of the posterior root depend for their nutrition upon the cells of the spinal ganglion, but a certain small proportion of them have their nutritive centres nearer to the periphery. So at least we may infer from the fact that some fibres die right through those portions of the root which are still attached to the ganglion on both its proximal and distal sides. The undegenerated fibres which should be found in the peripheral nerve have not been recognised as yet however. The difference between the fibres of the anterior and posterior roots, as regards their behaviour to section, has only been intelligible since *His*, *Froriep*, and *Beard* have shown us that while anterior roots grow out from the spinal cord, the spinal ganglia are formed from epiblastic thickenings outside and independent of the primitive neural plate, the cells of which give off processes which, growing inwards towards the cord and outwards towards the periphery, constitute the posterior roots and sensory nerves respectively.

If the degeneration method is to be made use of, it is desirable that the alteration in appearance presented by the dying nerves, and the time of onset of the successive phases in these alterations, should be understood.

In this investigation it is of the highest importance to bear in mind that, while the axis-cylinder is the process of a cell in the central system, the myelin-sheath by which it is surrounded is formed from many cells which have an independent, although probably epiblastic, origin.

Section of a nerve results in the death of its axis-cylinder. It seems, however, that as long as it lives the axis-cylinder exercises a restraining influence upon the nutrition of the myelin-cells by which it is surrounded; their tendency to form additional protoplasm, to grow and multiply is maintained at a minimum; their fatty metabolite, upon the existence of which depends their usefulness, is present in maximum quantity. When the axis-cylinder dies the myelin-cells enjoy a sudden exaltation of nutritive



activity, their protoplasm accumulates, their fatty metabolite is absorbed; their nuclei increase in size, develop regular active chromatin skeins and initiate cell-division. This condition of sur-activity soon begins to wane, accumulation of protoplasm ceases, the cells shrink and assume a stable form. Finally, the degenerated nerve comes to resemble a cord of connective-tissue.

A nerve-fibre has essentially the same structure whether it occurs within or without the axis. It consists of the real fibre, the cell-process or axis-cylinder, invested by myelin-cells, each of which is a hollow cylinder filled with phosphatic fat. While within the axis fibre and myelin-cells are supported by a neurogleia-sheath. When running through mesoblastic tissues, they are invested with a connective-tissue sheath, the sheath of Henle.

A peripheral nerve completely loses its irritability (in a warm-blooded animal) within forty-eight hours after section. Even by this time a distinct change is visible to the naked eye. Owing to the already-commencing accumulation of protoplasm in the medullary sheath, at first about the nuclei, with coincident absorption of myelin, the fibre looks less solidly white, and glistening. In about twenty days (*Ranvier*) the myelin only remains in drops, which here and there distend the sheath of Schwann.

Within the fresh cord a degenerated area is recognisable by the fifth week after injury as a milky patch. In three or four months it becomes less white, then grey, transparent and gelatinous in appearance (*Sherrington*). Finally, it is indistinguishable until after hardening of the cord. In the cord, hardened in bichromate of potassium, the degenerated area is visible at an earlier stage than in the fresh cord (in the cervical and dorsal regions in nine days—*Sherrington*) as an area lighter in colour and yellower than the surrounding white matter. For about the first six months after injury the distinctness of the degenerated tract increases. After this time it begins to shrink. In sections stained with carmine or acid fuchsin degenerative changes can be recognised in about a week (in the posterior columns in three days, in the lateral pyramidal tract in five, in the direct cerebellar tract in seven—*Homén*). At first the axis-cylinder appears thicker than normal and granular, and stains less darkly with carmine and more darkly than normal with acid fuchsin. The myelin-sheath begins to stain, especially at its inner part, more distinctly with carmine and less distinctly with acid fuchsin or Weigert's hæmatoxylin. Absorption of fat and proliferation of the myelin and neurogleia cells then ensues, in the same manner as already described for peripheral nerves. In a carmine-stained section the degenerated area is recognisable for a long period with a low power as a dark red patch, although its power of staining gradually diminishes.]

(*d.*) Essentially different to the methods we have just been describing is the plan introduced by *Gudden*, which also has yielded important results. There are points of similarity certainly between this method and the method of secondary degeneration; but in *Gudden's* method lesions are produced only on new-born animals (rabbits, puppies, and kittens). In such subjects the nervous system is still in a partly-embryonic condition,



and we have, therefore, arrested development as well as secondary degeneration combined in the results of the injury.

The still-growing cell-groups stand in quite a different relation to the destroyed conducting paths to that in which they would do if they belonged to a fully-developed functional organ which had already obtained a certain stability of structure. Accordingly we find that in a new-born animal the degeneration of the central end, as well as of its cells of origin, after the severance of a motor nerve is far more certain and complete than in one fully grown. We also find that, in the new-born animal, when one system is destroyed the degeneration may extend to a second, functionally dependent on the first. In this case it spreads from one neuron to another (*Monakow*), although in the second neuron it does not go so far as to absolutely destroy the tissue-elements.

An advantage not to be overlooked in this method of Gudden is the facility with which operative interference can be undertaken. The animals are easily handled. The readier coagulation of blood causes the bleeding to stop soon, even when large vessels are cut. The wounds heal quickly without suppuration. The animal is given back to the parent's care after the operation. It may be allowed to live for six or eight weeks, the longer the better, as a rule, and then it is killed and its central nervous system examined. A modification of this method is to tear the nerve out instead of dividing it. The successive changes then take place much more rapidly. There need be no fear of direct injury to the nerve-nucleus from the force employed (*Forel*).

Congenital or early-inflicted lesions of the central nervous system in human beings offer an analogy to these experiments.

*Mendel* has modified this method by choosing the muscles rather than the nerves for his point of attack. He destroyed single muscles or muscle-groups in new-born animals, and studied the consequent changes in the central nervous system.

There is no doubt but that in the future Gudden's operation method will greatly modify our views of the laws which govern degenerative processes.

#### 4. THE COMPARATIVE METHOD.

Since we can take for granted that the functional importance of an organ keeps pace with its anatomical prominence, we may expect many important disclosures from the comparative method.

First, we must study the system in the lower animals, in the hope that in them it will present a simpler organisation, and one, therefore, easier to understand than in man. *Edinger* has successfully combined the comparative and historical methods by examining the embryos of lower vertebrates.

The application of the comparative method to pathological processes in the central nervous system offers a wide and fruitful field for research. Further, one may take into consideration the fact that certain functions,



and the organs to which they belong, are not equally developed throughout the animal kingdom; the sense of smell is as deficient in man, for instance, as the sense of sight in the mole. The central organs associated with the senses above named must show a corresponding feebleness.

Animals which have strongly-developed hind-legs (jumpers) can be compared with animals with large fore-legs (diggers), and also with others, such as the whale, in which the limbs are rudimentary. *Meynert* first attributed to this kind of observation its proper merit. There are, however, many obvious differences in the relative importance of the several parts of the central nervous system in different animals, which we cannot yet bring into accord with their functional peculiarities.

## 5. PHYSIOLOGICAL METHOD.

All the methods by which injury is intentionally inflicted on animals might be included under this head; they have, however, been grouped with the injuries of disease. In the methods now under consideration we have to do with excitation or paralysis of muscles, resulting respectively from irritation and ablation of the brain or cord. For example, when a certain spot on the surface of the brain is stimulated, movement of a defined muscle-group results; or a particular region being excised, a sense organ is thrown out of gear. We may conclude that the part of the brain injured was in each case related to the organ over which it has lost its influence. No method, however, needs to be used with greater care, or leads more easily to mistakes.

The stimulation and the destruction of a part of the brain is apt to call into evidence not the part especially implicated, but some neighbouring region sympathetically set in action; or, again, unless the stimulus is appropriate it is apt to be ineffective. This is not, however, the place to point out all the mistakes which have occurred; we must content ourselves with showing that the value of physiological experiments must only be estimated in careful association with anatomical data.

Perhaps the condition of electrotonus may eventually be used for anatomical purposes.

The same results which we are able to produce in the central nervous system experimentally follow injury and disease; by the action of tumours, hæmorrhages, inflammation, etc., localised irritation and paralysis are induced, and the phenomena which result show the connection of the several parts of the system to one another. Even more caution is necessary in interpreting these results than in the case of injuries induced experimentally.

## 6. THE ANATOMICAL INVESTIGATION OF LIVING TISSUE.

All figures given by the foregoing methods of investigation are of altered tissue, in many cases even when a so-called fixing medium has been employed to preserve the structure.



The changes which take place in a nerve-cell during its functional activity have also been the subject of repeated experiment.

A great many methods of methylene-blue staining *intra vitam* have been proposed quite recently. Beautiful results can be obtained from mammals by the subcutaneous injection of considerable quantities of methylene-blue in solution. Fresh pieces of the central nervous system (which is stained blue throughout) should be placed for from two to four hours in a 10 per cent. solution of ammonium molybdate to which hydrochloric acid has been added in the proportion of 1 drop to every 10 c.c. (*Bette*), and kept at a temperature slightly above freezing point. They should then be well washed, hardened in alcohol, and cut.

The direct investigation of living nerve-tissue is always difficult and rarely successful; though *Ehrlich* has made a great advance by injecting a watery solution of methylene-blue (some 4.0 per cent. methylene-blue to 0.6 per cent. common salt, according to *Dogiel* and *Riese*) into the circulation. It stains the endings of the centripetal nerves and (for some minutes only) the ends of some centrifugal nerves. In the frog it suffices to inject the fluid into the spinal lymph-sac. Not all kinds of methylene-blue are equally efficacious; the best is that made in the anilin and soda factory at Ludwigshafen in Baden, or (according to *Edinger*) the *Methylenblau medicinale* from the Höchst factory (supplied by Merk). The blue colour appears only upon exposure to the air. After-treatment with iodide of potassium (*Pal*) or biniodide of potassium (*Smirnow*), or soaking in a mixture of equal parts cold saturated solution of ammoniated picric acid and glycerin (*S. Mayer*), renders the preparations more durable.

*Retzius* has very minutely investigated the central nervous system in invertebrates and obtained most successful stainings. He injected a considerable quantity of methylene-blue into the bodies of crabs and, having removed the shell, examined them an hour later, and again at regular intervals up to twelve hours, the times for the best results not being accurately determined.

He has also investigated the spinal cord of lower vertebrates (*Amphioxus* and *Myxine*) by direct application of the staining fluid.

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By the aid of the methods above mentioned, we have been able recently to throw much light upon the structure, hitherto but little understood, of the highest organs of the body. New methods are still wanted, however, to enable us to unravel the tangle of conducting paths.

None of the methods at present in use will stand a strict criticism, and the same want may be anticipated in the case of methods devised in future. If it is recognised that no single method is sufficient in itself, but that all must be used in conjunction, a thorough exploration of the nerve paths may be finally counted on. Experience teaches us that



the introduction of any good method has invariably meant a great step forward, and consequently it can be held no idle task to further the study of methods.

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## SECTION II.—MORPHOLOGY OF THE CENTRAL NERVOUS SYSTEM.

IN fresh preparations the difference in colour between the grey and white substances is sufficiently marked for anatomical purposes.

Previous hardening in alcohol gives to the soft nerve-mass a consistence which facilitates its handling, and, at the same time, brings out certain minute details in configuration more clearly or, at least, more permanently. The great disadvantage of alcohol-preparations is the loss of the natural colour.

[The following method of bringing out the grey and white matter in strong contrast is sometimes useful for class demonstrations:—Slices of spirit-brains, complete coronal sections for example, are placed in a watery solution of tannin or gallic acid; they are then washed for about an hour in running water, after which they are immersed in a solution of ferrous sulphate for a few minutes, and again washed. The large quantities of proteids in the grey matter fix the gallic acid, which subsequently combines with the iron. Very striking differentiation is thus obtained, but the black staining is seldom restricted to the grey matter; it is apt to sink into such bundles of fibres as are transversely cut.]

Brains hardened in bichromate of potassium, and subsequently, after the chrome-salt is washed out in water, placed in alcohol, are useful for macroscopic work. The grey matter is very sharply defined and the chrome-salts effect a staining which varies with the direction and thickness of the nerve-fibres. During the process of hardening the brain, all pressure or traction upon the tissue must be prevented by careful support with cotton-wool and by the use of vessels of suitable form.

The differences in colour are made most visible if the preparations, after a month's hardening in Müller's fluid, are placed in alcohol, to which 1 per cent. of hydrochloric acid is added. Pieces so treated preserve for a long time in glycerin their characteristic green staining (*Agono* and *Beisso*). Formaldehyde (formol from Meister, Lucius & Brüning's dye-works) diluted with ten times its own bulk of water is an excellent medium for preserving the central nervous system. The preparations are less hard than those made in alcohol, and very little shrunken; and, except for the blood-pigment, they keep their natural colour. Sections of them can be treated by many staining methods, Weigert's included. The various discomforts attending the use of wet preparations, such as the smell, the fumes of



alcohol, the wetting of the fingers in handling them, have led to the introduction of dry methods, which are useful at least for the study of external form.

*Schwalbe's* method of preparing dry brains is to be recommended. They are hardened in zinc-chloride or spirit (if in zinc-chloride they must be thoroughly washed), dehydrated in strong alcohol (96–97 per cent.), placed in turpentine for about eight days, then in melted paraffin. The best paraffin for the purpose melts at from 45° to 50° C. They lie in the paraffin in an incubator for from five to eight days, by which time they are thoroughly soaked. The paraffin is allowed to drain off, and the preparation to cool in the position which best prevents distortion. These preparations are yellow or light brown in colour, but extremely permanent and clean; they are exactly like wax models in appearance.

## ANATOMICAL TERMINOLOGY.

In the following account the terms 'outer, inner, above, below, anterior, posterior' will only be employed in cases in which the use of the terms has become so universal as to be unavoidable without ambiguity; for instance, the 'anterior' and 'posterior nerve-roots.'

The brain being looked upon as the centre we shall speak of proceeding towards it as proceeding brainwards or proximally, and away from it as travelling caudalwards or distally. The terms dorsal, ventral, lateral, and mesial (nearer to the middle line), and median (in the middle line) need no explanation.

## DEVELOPMENT.

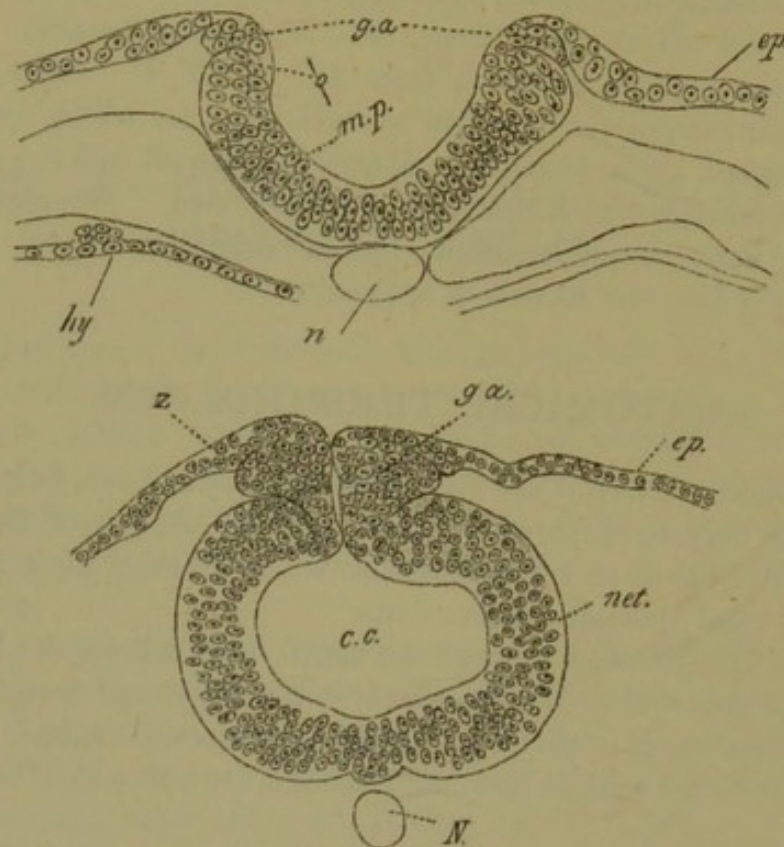
[The portion of the epiblast which is marked out as the seat of origin of the central nervous system constitutes the floor and sides of the medullary groove. It is not simply a uniform plate, but the central portion, out of which the spinal cord will be formed, is distinct from a row of thickenings which lies on either side of the large main fossa. It is these lateral thickenings of the epiblast which develop into the spinal ganglia (*His*).

The medullary folds grow up until, meeting in the mid-dorsal line, they convert the medullary groove into a canal. Closure occurs in the neck region first, and spreads rapidly forwards over the head and more slowly backwards through the dorsal, lumbar, and sacral regions. The rudiments of the sensory ganglia (both cranial and spinal) are formed by delamination from the lateral thickenings just described (*Beard*). When the medullary plates meet in the mid-dorsal line these thickenings are left outside the neural canal, or rather, to define their situation more accurately, they are just caught within the approaching lips of the medullary plate and rest upon the dorsal surface of the neural tube. Afterwards they sink down into their permanent positions on either side of the cerebro-spinal axis.

The whole of the central nervous system is formed from epiblast, and as the rest of this layer becomes the skin and sense organs, the portion of it which is set aside for the nervous system may be distinguished as neuro-



epithelium. The layer of neuro-epithelium is at first only one cell thick, later on it becomes many layered, owing to proliferation of its cells; but it is particularly noticeable in sections which are stained, so as to bring out the chromatin figures of the nuclei, that these exhibit the changes which



Figs. 1 and 2.—Transverse sections through a developing chick, showing the formation of the sensory root-ganglia (after Beard).—*ga*, Ganglia; *ep*, epiblast; *hy*, hypoblast; *m.p.*, medullary plate; *n*, notochord; *net.*, neuro-epithelial tube; *c.c.*, central canal.

usher in cell division only in the cells which lie next to the central canal of the spinal cord, and in the case of the brain near its surface (cortex) as well as next to the ventricles.

In his recent researches, *His* has shown that even at the time when the neuro-epithelium constitutes but a single layer, the cells composing it are

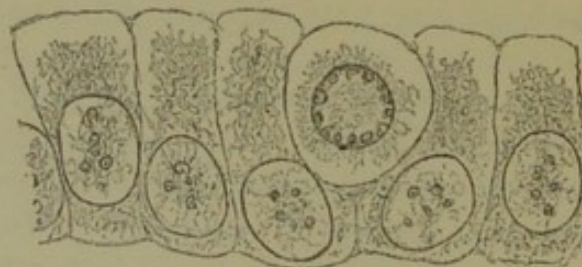


Fig. 3.—The epiblast involuted to form the central nervous system while still a single layer, rabbit (after *His*). A round germ-cell lies between the proximal ends of two supporting cells.

distinguishable into two classes. Although they all belong to the same layer, they exhibit from the first a distinction into the more important cells, 'germ-cells,' which develop into nerve-cells, and the 'spongioblasts' or supporting cells. The spongioblasts are elongated, palisade-like cells,



the oval nuclei of which lie at some distance from the central canal. The germ-cells are round protoplasmic cells which lie amongst the inner non-nucleated segments of the spongioblasts (figs. 4, 4a).

As the spongioblasts become more elongated, their nuclei sheer over one another, but the supporting tissue of the system is formed by cells which reach throughout its whole thickness. The substance of these cells is not homogeneous, but consists of a formed part disposed in filaments and a soft transparent substance in which the filaments are embedded. The fibrillar elements are disposed so as to form a membrane, the 'internal limiting' membrane which supports the epithelium of the central canal,

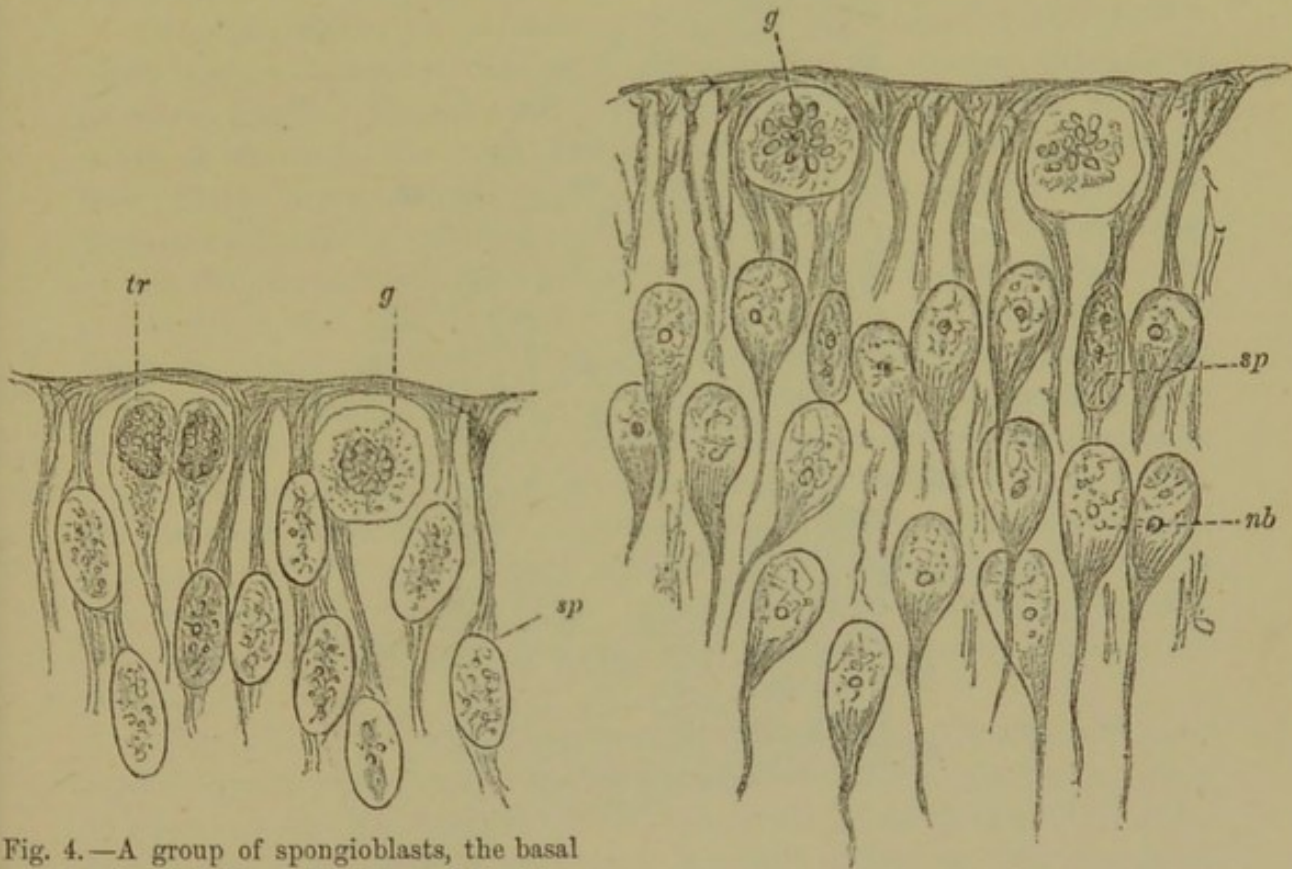


Fig. 4.—A group of spongioblasts, the basal ends of which form the internal limiting membrane (after *His*).—*g*, Germ-cell; *tr*, cells transitional between germ-cells and neuroblasts; *sp*, spongioblasts.

Fig. 4a.—Similar to 4 but somewhat more advanced. The neuroblasts (*nb*) are giving off axis-cylinder processes.

and they also constitute the scaffolding for both grey and white matter. Throughout the grey matter the spongioblasts are disposed radially with tangential or oblique connecting bands. When they reach the outside of the grey matter, they break up into a close irregular plexus, the 'border veil,' as *His* has called it (an expression which may be Latinised as 'velum confine'), because it prevents the migration farther outwards of the neuroblasts, while it gives passage to their processes. It is along this close outer network that the longitudinally-running fibres are directed, and it consequently becomes the scaffolding of the white matter also.

The nerve-cells, on the other hand, are formed by the division of the germ-cells, the daughter-cells of which, becoming pyriform, are termed



'neuroblasts.' For some considerable time the neuroblasts have one process only, the axis-cylinder process, which is directed outwards towards the anterior roots of the nerves. Subsequently the neuroblasts develop lateral dendritic processes.

In the earlier stages of development the cerebro-spinal axis is altogether occupied in forming motor-cells and fibres. Its neuroblasts take no part in the formation of sensory nerves. The fibres of the posterior root arise as outgrowths of the cells of the ganglia. These cells are at first bipolar; one of their processes extending outwards into the sensory nerve, the other

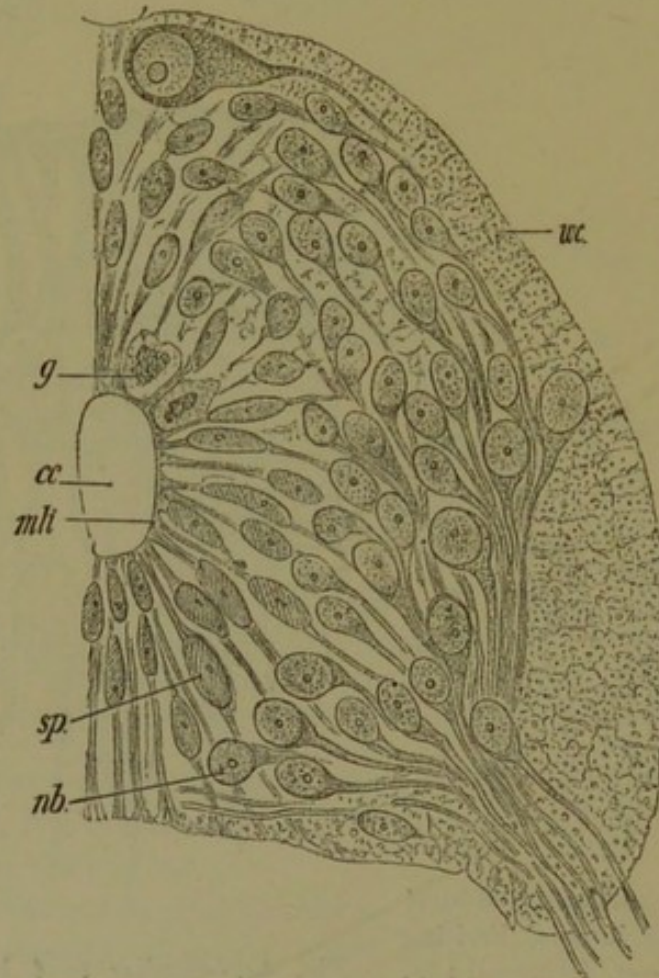


Fig. 5.—Transverse section of half the spinal cord of a trout-embryo (after *His*).—*c.c.*, Central canal; *mli*, membrana limitans interna; *g*, germ-cell; *sp*, spongioblast; *nb*, neuroblast; *wc*, white columns, of which the supporting tissue is a close network formed from the ramifications of the outer segments of the spongioblasts.

inwards to the cord. Subsequently the centripetal and centrifugal processes are placed in direct continuity by the cell body withdrawing itself away from them at right angles. Thus while the cells continue to provide for the nutrition of the fibre through the vertical limb of the T, the passage of the afferent impulses through its body is rendered unnecessary.

The account of the early stages in the histogeny of the cells given by *His* still leaves some points unsettled, as, for instance, the origin of small nerve-cells and granules, as well as the neuroglia-cells of Deiters, unless these are all derived from spongioblasts. A similar obscurity



enshrouds the origin of the myelin-cells that invest the axis-cylinder processes of the neuroblasts.

The origin of the neurogleia-cells has been much debated. By some they have been considered as immigrant-cells, white blood-corpuscles, or cells of connective-tissue rank, but *Vignal* concludes from his observations that they, like the nerve-cells, are epithelial derivatives.

In the spinal cord, motor nerve-cells are recognisable as such at the tenth week of intra-uterine life. They make their appearance in two principal groups corresponding to the anterior and lateral horns. As already remarked, the fibres of the posterior root are outgrowths of cells which lie in the sensory ganglia outside the cerebro-spinal axis.

Although dilated at its anterior end into the brain, the grey matter which borders the central canal is formed in the same manner throughout its whole length. Beneath the lining epithelium lies the layer of cells, which, as shown by the form and prominence of the chromatin-skeins in their nuclei, are undergoing active proliferation into nerve-cells. From the nerve-cells fibres extend outwards as motor nerves. It seems pretty certain that these fibres (axis-cylinders) extend without a break from the nerve-cells in the axis in which they take origin to the striated muscle which they innervate; the fibres destined for involuntary muscle, on the other hand, reach, in the first instance, to cells of sympathetic ganglia only, and are by means of these broken up into a number of finer filaments. Inside the cerebro-spinal axis, as well as throughout their peripheral course, the fibres are supported by myelin-cells, which, wrapping themselves round the axis-cylinder, develop in their substance a special phosphatic fat, and in this way constitute protecting and insulating tubes. Whether the myelin-cells arise from epiblastic or mesoblastic elements has not been as yet determined.

While within the central nervous system the axis-cylinders and their myelin-sheaths are supported by the neurogleia, and it is almost necessary to point out that the origin of the myelin-sheath of intra-axial fibres is far from clear, if, as asserted by *Boveri*, it is not broken up into segments. *Schiefferdecker*, on the other hand, states that 'nodes of Ranvier' are to be found within as well as without the cerebro-spinal axis.

The white columns appear later than the grey matter. Their origin has not as yet been satisfactorily made out. Probably the motor fibres grow downwards from cells of the cortex, while sensory fibres originate in cells of the cord and grow upwards.

The anterior end of the involuted tube of epiblast is dilated into the cerebral vesicles (fig. 5). From the anterior vesicle the cerebrum grows out as a secondary fore-brain. At first this new vesicle is single, but it soon divides into two, each communicating with the primary fore-brain by an aperture, the foramen of *Monro*. The formation of grey matter within the secondary vesicles is confined to the posterior and inferior parts of the wall of the ventricle. Here, however, it occurs extensively as the corpus striatum, which bulges into the ventricle, and is divided into two parts by a deep groove. The optic thalamus and corpus striatum are, therefore,



widely separate in their origin, the former being a local development of the grey matter bordering the primary fore-brain, while the latter is formed in the wall of the secondary vesicle.

But little remains to be said with regard to the further development of the central grey matter—the formation of neuroblasts from the cells of its inner layer—their migration outwards—the radiation of their processes towards the periphery—the investment of the grey matter with a sheath of longitudinal fibres occur throughout its whole length. In the case of the brain, on the other hand, the seat of the chief formative activity is transferred to the surface of the vesicles where the neuroblasts, which are afterwards to become the cells of the cortex of the cerebrum, corpora quadrigemina and cerebellum, commence their existence.

To follow all the changes in the walls of the cerebral vesicles by which the formation of the brain is accomplished would require a special treatise on embryology, nor can the task be attempted at present owing to the incompleteness of our knowledge, but certain points which have the most important influence upon our conception of the fundamental structure of the central nervous system may be briefly referred to.

The cranial nerves are formed in the same way as the spinal nerves, their motor fibres being outgrowths from cells of the central grey matter, the sensory fibres originating in cells of the sensory ganglia, and growing inwards into the central grey matter and outwards to the surface. To this description the olfactory and optic nerves do not seem, at first sight, to correspond, for both these cranial nerves, or rather the 'tracts,' by means of which their connection with the brain is established, appear as hollow outgrowths from the brain; the optic vesicles being diverticula of the fore-brain; the olfactory vesicles being, apparently, diverticula of the hemispheres of the secondary fore-brain. In the case of the olfactory tracts, an earlier stage, in which they were connected with the dorsal wall of the primary fore-brain in the same manner as other sensory nerves, has been described by *Marshall*. The relation of the first two cranial nerves to the central system is, however, complicated by the fact that elements, which elsewhere lie in the sensory ganglia and cerebro-spinal axis, viz., bipolar cells, 'gelatinous' substance, and multipolar cells, are situated in the olfactory bulb and retina in immediate juxtaposition with the epithelium of the sense organs. There appears to be this great phylogenetic difference between the nose and eye and other sense organs that, owing to their situation at the anterior end of the body and consequent advantages for obtaining information, they very early became highly specialised, and the portion of nerve plexus which lay beneath them was so intimately united to them that its subsequent withdrawal into the axial system, as in the case of other segmental sense organs, was impracticable.

The roof of the anterior cerebral vesicle and the back part of that of the posterior cerebral vesicle (fig. 6, *Zh* and *Nh*) remain undeveloped. The ventricular epithelium is simply supported by pia mater, in which ramify the vessels of the choroid plexus. The roof of the anterior vesicle is a flat plate, triangular in shape, the 'velum interpositum.' The hemispheres



of the cerebrum project backwards, and press up against the sides of the anterior vesicle. Where they touch the margins of the velum interpositum this membrane grows out sideways, pushing the wall of the secondary fore-brain in front of it, and so involuting it into its ventricle, where it rests as a free fold upon the corpus striatum. In this way a choroid plexus is carried into the lateral ventricles, the velum interpositum being grasped by the wall of the cerebral hemisphere from the back of the foramen of Monro to the uncus. By the subsequent downward growth of the hemisphere, as well as the increase in thickness of the crus cerebri, the postero-external angle of the velum interpositum is carried downwards and forwards round the crus. If the finger were placed beneath the wing of a butterfly to represent the crus cerebri, and the back of the wing were then bent downwards round the finger, the form of the velum interpositum would be accurately represented. The margin of the curved slit, through which it pushes its way into the lateral ventricle, is thickened by longitudinal fibres. The bundle on the convexity of the slit is the fornix. The bundle in its concavity is the stria cornea.

The pineal gland arises as a hollow outgrowth from the back of the roof of the fore-brain; the pituitary body as a hollow downgrowth from its floor which applies itself to the back of a diverticulum from the buccal cavity, which comes up through the hole in the floor of the pituitary fossa of the sphenoid bone.

The corpus callosum is, in its full development, a secondary growth which breaks through the wall of the hemisphere, sweeping away the greater part of the arcuate convolution of Arnold. Its anterior end is first formed and growth proceeds from before backwards. The remains of the arcuate convolution are seen in the striæ medullares *seu* obtectæ, or nerves of Lancisi, and in the subcallosal (subgenial and subsplenic) convolution. The portion of the wall of the hemisphere, which is intercepted between the corpus callosum and the fornix, remains undeveloped as the septum pellucidum or wall of the so-called fifth ventricle.\*]

### DIVISIONS OF THE CENTRAL NERVOUS SYSTEM.

From the earliest time the system has been described as the elongated **spinal cord** (*medulla spinalis*), and the more massive and globular **brain** (*cerebrum* in its wider sense or *encephalon*).

The brain is again subdivided into great brain (*cerebrum*), small brain (*cerebellum*), and *medulla oblongata*. Usually the *medulla oblongata* is regarded as the segment between the proximal end of the spinal cord and the pons Varolii, the latter being looked upon as belonging to the *cerebellum*. Some anatomists (*e.g.*, *Merkel*) include the pons with the *medulla oblongata*. The part in front of the pons belongs to the great brain.

The division most widely accepted nowadays is based upon develop

\* For a more detailed account of the development of the brain, see *Quain's Anatomy*, Tenth Edition, vol. i. part 1.



mental study. Hence it follows that a knowledge of the leading features, at least, of the *development of the central nervous system* has become an absolute necessity.

The first rudiment of the entire nervous system is the medullary plate, a long-drawn thickening in the middle line of the epiblast (ectoderm). Next, this medullary plate assumes the form of a groove, the medullary groove, by the rise of two parallel ridges, the medullary folds, which continue to grow as development progresses until, meeting in the mid-dorsal line, they convert the groove into a canal. The hinder and longer part of this canal is the rudiment of the spinal cord; the other, which lies in the head region of the embryo and appears to be closed in front, is the rudiment of the brain. From the epiblast the rudiments of the spinal ganglia also develop, probably by delamination from the lateral thickenings (the medullary folds), and during the later stages rest in two parallel rows on the dorsal surface of the neural tube.

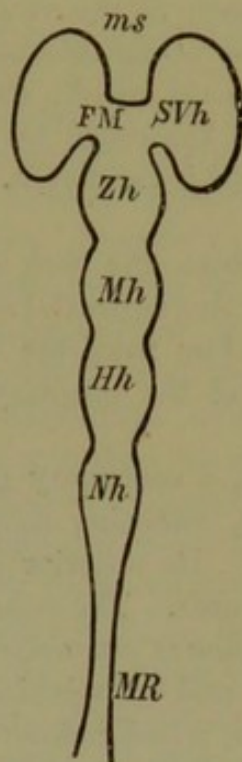


Fig. 6.—The cerebral vesicles.—  
SVh, Secondary fore-brain;  
Zh, 'tween-brain; Mh, mid-brain; Hh, hind-brain; Nh, after-brain; ms, longitudinal fissure; FM, foramen of Monro; MR, central canal.

In the brain part of the neural tube (in mammalia even before its complete closure) several shallow depressions are visible, which divide this part first into four and then into five segments, lying one behind the other. The divisions are named from before backwards: the primary anterior cerebral vesicle (Zh), the middle cerebral vesicle (Mh), the anterior (Hh), and the posterior (Nh) of the two hinder vesicles. Later on, a fifth vesicle, the secondary anterior vesicle, grows out from the anterior wall of the primary fore-brain, the lamina terminalis of the embryo. This too is single at first, but is soon divided from before backwards by the downgrowth of the primary falx, SVh. In the human embryo this takes place in the fourth week of foetal life. The fissure is known as the longitudinal fissure, ms.

I should have mentioned before that at a very early period, as soon, indeed, as the first signs of differentiation are perceptible in the brain part of the tube, two lateral vesicles begin to spring from the under surface of the fore-brain. These are the rudiments of the eyes and the nervus opticus, the primary eye-vesicles.

In higher vertebrates the secondary anterior vesicles make by far the most rapid growth of all the divisions of the rudimentary brain; they represent the cerebrum in its rudimentary state.

The differentiation of the original neural tube can be traced throughout the whole series of vertebrates. In the rays alone no secondary



fore-brain is said to be formed, while in other selachians we find the mere rudiment of one (*Edinger*).

The several portions of the brain are developed from one or other of these five divisions:—

1. **Secondary anterior cerebral vesicle** (*SVh*) forms the cerebrum with its cortex, corpus callosum, fornix and anterior commissure, nucleus lenticularis, and nucleus caudatus.

2. **Primary cerebral vesicle** (*Zh*), or 'tween-brain, includes the optic thalami, infundibulum, optic commissure, and corpora albicantia.

3. **Middle cerebral vesicle** (*Mh*) forms the mid-brain; corpora quadrigemina and peduncles of great brain.

4. **The anterior of the two hinder vesicles** (*Hh*) forms the hind-brain; cerebellum with its peduncles and the pons.

5. **Posterior of the two hinder vesicles** (*Nh*) forms the after-brain or medulla oblongata.

All the structures developed from the secondary anterior vesicles belong to the cortex or brain-mantle, while the structures to which the remaining four vesicles give rise constitute, with the exception of the cerebellum, the brain-stem (caudex). The nuclei lenticularis et caudatus are included, for the most part, in the description of the brain-stem, leaving only the cortex of the great brain for the mantle-formation; recently, however, it has been shown that the nucleus caudatus, as well as the lateral part [and perhaps the central part too] of the nucleus lenticularis, ought to be included amongst cortex-formations.

[The morphological relation of the cortex to the rest of the cerebro-spinal axis is a matter of the greatest importance, involving, as it does, the question of the primary constitution of the nervous system. The brain is distinguished from the spinal cord by the possession of an envelope, not complete, but covering the greater part of the surface of its three vesicles, as the cortex or mantle-formation. Throughout the whole system the 'axis' consists of a tube of grey matter bordering the central canal, invested by a sheath of longitudinally running white fibres. *Meynert* recognised the continuity of the grey matter bordering the central canal, and termed it 'centrales Höhlengrau,' without, however, giving to the term any strict morphological or anatomical limitations. From the translator's point of view, all the grey matter of the lower system, including therein the optic thalami, constitutes the central grey tube. This receives sensory, and gives origin to motor nerves, none of which appear to pass through its plexus without joining with it, but each nerve terminates in, or springs from, the portion of the grey matter belonging to the metamer which the nerve supplies. In its fore part the nervous system is dilated into the vesicles already described, and here a marked difference in anatomical arrangement is seen. The white matter which invests the central grey tube is in turn surrounded by a layer of grey matter of altogether different constitution. This second investment constitutes the cortex of the cerebellum, corpora quadrigemina, and cerebral hemispheres. In the lowest vertebrates the cerebellum is, as a rule, small; although, even



amongst fishes, it may attain, as in the shark for instance, a considerable size and complex structure. The corpora bigemina are larger proportionally in lower vertebrates than they are in man. The cortex of the cerebrum is, however, a late development; only in mammals does it constitute an important layer. In reptiles and birds the mass of the cerebral hemisphere consists of what in mammals we know as corpus striatum. Does the corpus striatum belong to the central or the peripheral grey tube? It does not, like the optic thalamus, contain the primary centres of any sensory nerves. The nucleus caudatus is intimately connected with the cortex, for its head, as shown in the accompanying diagram after *Wernicke*, rests on the anterior perforated space, its tail is continuous with the cortex of the temporal lobe.

Nucleus caudatus, nucleus amygdaleus, and claustrum are continuous at their temporal extremities. The nucleus lenticularis is sunk more deeply beneath the cortex, and completely invested in white matter. In structure and development, however, the lenticular and caudate nuclei strongly resemble one another, and all the evidence we at present possess is in favour of assigning them both to the same position in the system, as parts of the peripheral grey tube.

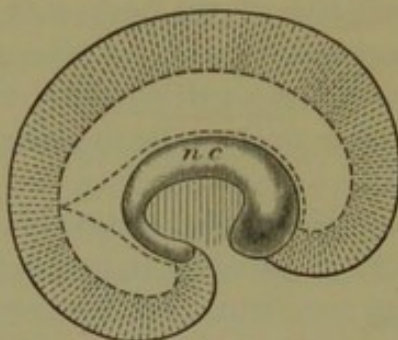


Fig. 7.—Diagram representing the connection of the nucleus caudatus with the cortex of the frontal and temporo-sphenoidal lobes.

The optic thalamus, on the other hand, is to be regarded as the anterior extremity of the central grey tube.]

The entrance into the lateral vesicles from the fore-brain constitutes eventually the foramen of Monro; the cavities of the brain vesicles remain as the permanent **ventricles**.

The cavity of the secondary fore-brain becomes the lateral ventricle.

„	„	primary fore-brain	„	the third ventricle.
„	„	mid-brain	„	the aqueduct of Sylvius.
„	„	hind-brain	„	the fourth ventricle.
„	„	medullary canal	„	the central canal.

*His* has divided the brain somewhat differently; into (1) Rhombencephalon, which includes the after-brain, hind-brain, and isthmus (the narrow part in front of the pons); (2) Mesencephalon, the mid-brain; (3) Prosencephalon; this last being subdivided into Diencephalon, the 'tween-brain, and Telencephalon, the secondary fore-brain.

The several divisions of the central nervous system indicated in the account just given will be briefly passed in review in this section.



## A. THE SPINAL CORD.

The human spinal cord (figs. 8 and 9) forms a cylindrical column of 38 to 46 cm. (18 inches) in length, reaching in the upright position from the first cervical to the first or second lumbar vertebra. In the child it reaches farther [the third lumbar at birth]. In the fœtus farther still. When the body is bent sharply forwards the lower end of the cord in the adult only reaches to the twelfth dorsal vertebra. *Heger* determined that when the body is strongly bent the spinal cord is stretched by 6·8 per cent. of its length.

In two situations it presents spindle-shaped swellings, due almost entirely to an increase in its transverse diameter. In thick specimens the first of these, the cervical swelling (*intumescencia cervicalis*), has at the level of the fifth or sixth cervical vertebra a breadth of 15 mm.; the lumbar enlargement lying at the level of the lower dorsal vertebræ attains a breadth of 11 to 12 mm. The antero-posterior diameter increases in these situations by 1 to 2 mm. only.

The thickness of the cord varies considerably in different individuals; treating its cross-section as a complete circle, one finds that the diameter of this circle above the cervical swelling varies from 8 to 11 mm.; in the dorsal cord, between the two swellings, from 6 to 9 mm.

The lumbar swelling (*intumescencia lumbalis*) terminates in the *conus medullaris*. The latter forms the end of the cord. To it, however, is attached a thin thread of some 25 cm. in length, the *filum terminale*.

*Flesch* has shown that the cord is so constituted as to present—after the removal of the pressure of the vertebræ—the curves which are seen in it when *in situ*.

Down the middle line of its ventral surface runs a furrow, *sulcus longitudinalis medianus anterior* (fig. 8, *Fsla*), cut so deep into the cord as to form a longitudinal fissure, *fissura mediana anterior*. Another furrow runs down the middle line of the dorsal surface, *sulcus longitudinalis medianus posterior* (fig. 9, *Fslp*), but as this latter penetrates the substance of the cord very slightly or not at all, the term 'fissure,' as applied to it, is incorrect.

The dorsal roots originate in an almost uninterrupted line 2 to 3 mm. laterally to the posterior fissure. When they have been cut away, the place of their origin is still indicated by a furrow, the dorso-lateral groove, *sulcus lateralis dorsalis* (*Sld*), *sillon collatéral postérieur*. It is shallow for the most part but somewhat deeply cut into the cord in the cervical region. The anterior roots arise in many separate bundles spread out transversely as well as longitudinally. The furrow left after their removal (the so-called antero-lateral groove), *Slv* (fig. 10), is very indistinct. The roots incline on leaving the cord caudally as well as laterally, the inclination downwards being sharper the lower their situation on the cord. An exception to this rule is observed in the course



taken by the most posterior root-bundles of the upper cervical nerves, which necessarily turn a little brainwards: as also in the course of the roots of the nervus accessorius Willisii which arise from the lateral

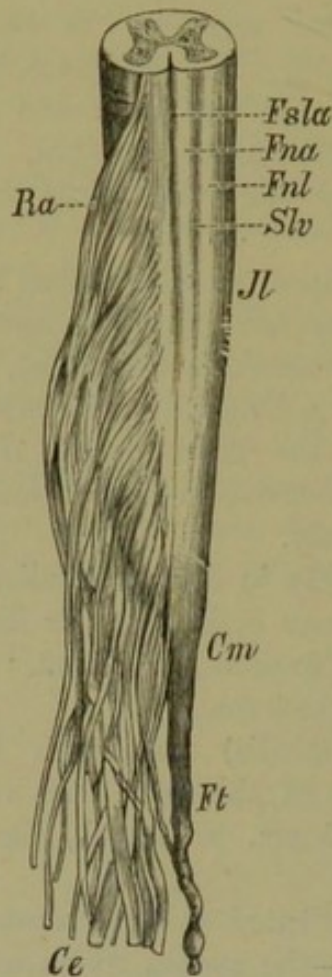


Fig. 8.—Caudal end of spinal cord from ventral surface (*natural size*).—*Jl*, Lumbar enlargement; *Cm*, conus medullaris; *Ft*, filum terminale. The anterior nerve-roots on the left side are removed, on the right side (*Ra*) they enter into the formation of the cauda equina (*Ce*). *Fsla*, fissura longitudinalis ant.; *Slv*, sulcus lateralis ventralis; *Fna*, funiculus anterior; *Fnl*, funiculus lateralis.

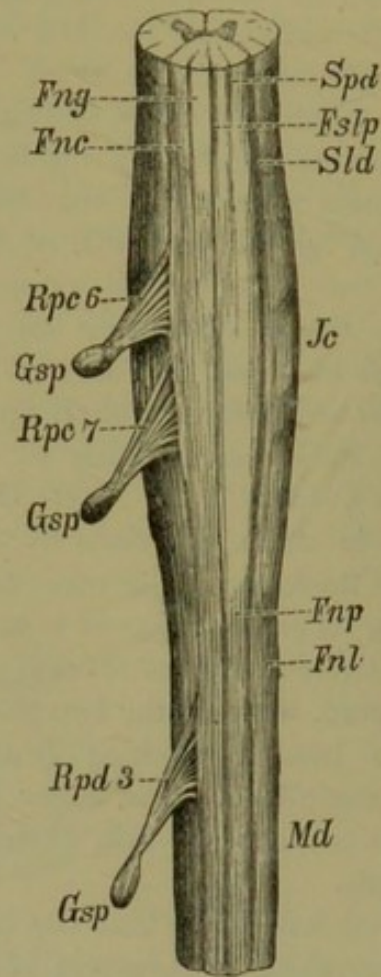


Fig. 9.—Cervical enlargement of the spinal cord from the dorsal side (*natural size*). Besides the cervical enlargement (*Jc*) a portion of the dorsal cord is also visible (*Md*). All the posterior roots are cut away on the right side, and on the left side the sixth and seventh cervical (*Rpc* 6 and 7) and the third dorsal (*Rpd* 3) are left as far as the spinal ganglia (*Gsp*). *Fslp*, Fissura longitudinalis post.; *Spd*, sulcus paramedianus dorsalis; *Sld*, sulcus lateralis dorsalis; *Fnp*, funiculus posterior; *Fnl*, funiculus lateralis; *Fng*, funiculus gracilis; *Fnc*, funiculus cuneatus.

surface of the cord between the posterior and anterior roots. By the time the lumbar swelling is reached the roots lie almost parallel with the cord; the conus medullaris and filum terminale lie in the middle







more distinct as we travel cerebralwards, the sulcus paramedianus dorsalis seu intermedius posterior, *Spd*.

The cord is divided by these furrows into several longitudinal columns distinct from one another on the surface.

1. Anterior column, funiculus anterior, *Fna*, lying between the anterior fissure and the line of exit of the anterior roots.

2. Lateral column, funiculus lateralis, *Fnl*, on the outer side of the anterior column, between this and the postero-lateral sulcus.

3. Posterior column, funiculus posterior, *Fnp*, between the posterior longitudinal and dorso-lateral sulci. In those regions in which a paramedian sulcus is visible, the posterior column is again divided into two, Burdach's column, *Fnc* (funiculus cuneatus); and Goll's column (funiculus gracilis), *Fng*.

Usually 31 pairs of spinal nerves are reckoned, viz., 8 cervical, 12 dorsal, 5 lumbar, 5 sacral, and 1 pair of coccygeal nerves. One or two microscopical coccygeal nerves may be usually found, however, in the filum terminale (*Rauber*).

In most vertebrates the spinal cord is rounded, as in Man, but in many fishes we find it in transverse section, shaped like an obtuse-angled triangle with the apex dorsalwards. In cyclostome fishes it is ribband-shaped, the flattened edges being curved slightly ventralwards. The swellings occur in almost all vertebrates, and are proportionate in size to the masses of roots which spring from the cord. Thus we find the cervical swelling very strongly marked in long-armed apes, while the swellings are hardly perceptible in the spinal cord of Cetacea, and entirely lacking in that of snakes. In many vertebrates the cord occupies the whole length of the canal, leaving no room for the formation of a cauda equina; in others (as Cheiroptera, hedgehog) it is proportionately much shorter than in Man, and in some fishes (*Lophius piscatorius*, *Orthogoriscus mola*) it is reduced to a mere short appendage of the brain.

In Birds the posterior columns diverge in the lumbar region, leaving a wide rhomboidal cleft (sinus rhomboidalis posterior) which is filled with a peculiar gelatinous substance.

## B. THE BRAIN.

### I. THE AFTER-BRAIN.

The cross-section of the system increases very rapidly in its transverse diameter in front of the first cervical nerve. The spinal cord forms into the **medulla oblongata**. This reaches to the back of the great cross-fibres of the pons (figs. 11 and 12, *Po*). It attains a length of about 3 cm. On the surface of the medulla several details in moulding are to be noticed. We will describe the furrows first. For the most part the furrows are longitudinal, and continue upwards the sulci of the cervical cord.



The anterior fissure, *Fsla* (fig. 10), extends on the ventral surface as far as the back of the pons; it is very shallow in the lower part, but deepens in front, and ends at last, where the pons fibres cross, in a blind hole, foramen cæcum posterius, *Focp*.

A rather shallow fissure forms an acute angle with the anterior fissure at the hinder end of the medulla, and extends forwards as far as the border

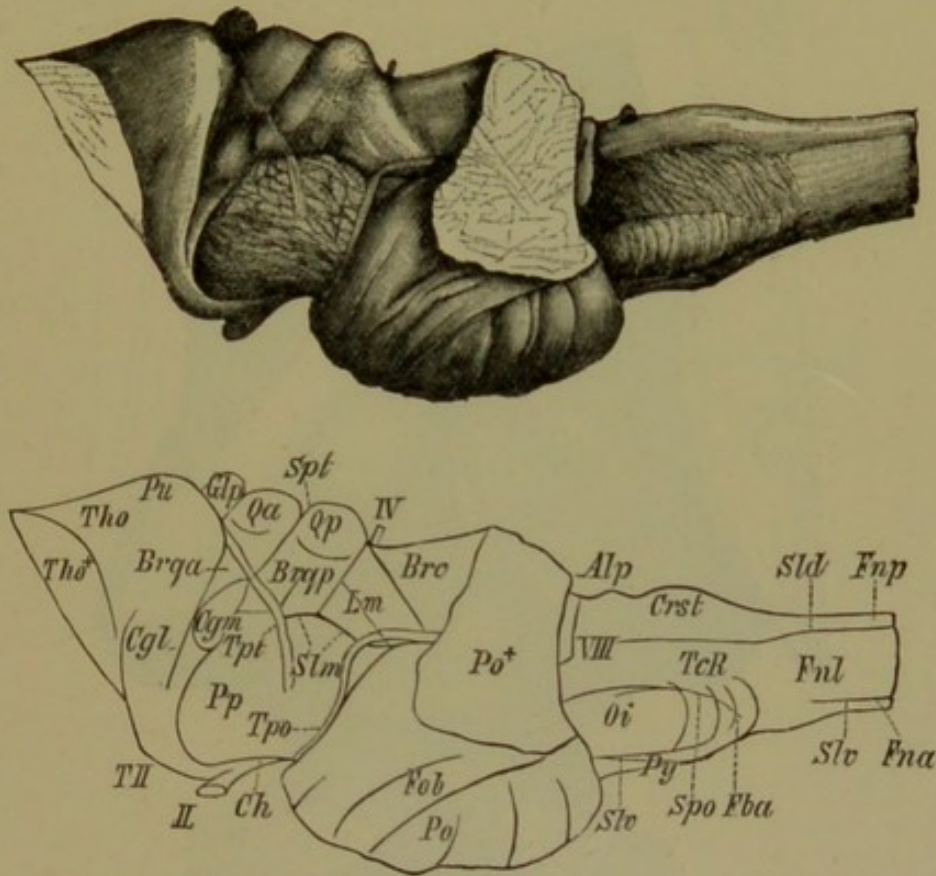


Fig. 11.—A preparation similar to that in fig. 10, seen from the left side (*natural size*). Nerve roots are for the most part cut away.—*II*, Nervus opticus; *IV*, trochlearis; *VIII*, acusticus; *Alp*, ala pontis; *Brc*, brachium conjunctivum (superior cerebellar peduncle); *Brqa*, anterior brachium; *Brqp*, posterior brachium; *Cgm*, corpus geniculatum mediale; *Cgl*, corpus geniculatum laterale; *Ch*, chiasma nervorum opticorum; *Crst*, corpus restiforme; *Fba*, fibræ arcuatae; *Fna*, funiculus anterior; *Fnl*, funiculus lateralis; *Fnp*, funiculus posterior; *Fob*, funiculus obliquus; *Glp*, glandula pinealis; *Lm*, lemniscus or fillet; *Oi*, inferior olive; *Po*, pons, cut across at *Po+*; *Pp*, pes pedunculi; *Pu*, pulvinar thalami; *Py*, pyramid; *Qa*, corpus quadrigeminum anterior; *Qp*, corpus quadrigeminum posterior; *Sld*, sulcus lateralis dorsalis; *Slm*, sulcus lateralis mesencephali; *Slv*, sulcus lateralis ventralis; *Spo*, sulcus postolivaris; *Spt*, sulcus corp. quad. transversus; *TII*, tractus opticus; *TcR*, tuberculum cinereum Rolandi; *Tpo*, tenia pontis; *Tpt*, tractus peduncularis transversus; *Tho*, thalamus opticus, cut at *Tho+*.

of the pons, sulcus parapyramidalis, *Sppy*. The furrow corresponding to the anterior roots, hardly to be seen in the cord, is more distinct in some parts of the medulla oblongata, sulcus lateralis ventralis (*seu* internus olivæ *seu* hypoglossi), *Slv*. Here and there, however, it is obliterated by crossing fibres.

The following sulci belong to the dorsal surface (figs. 11 and 12):—1,



Sulcus lateralis dorsalis, *Sld*; 2, sulcus paramedianus dorsalis, *Spd*; 3, in the middle line, posterior longitudinal or dorsal fissure, *Fslp*. The first two incline laterally up the medulla, the sulcus lateralis can be followed to the pons, the sulcus paramedianus soon disappears. The fissura long. dors. ends suddenly where the central canal opens out into the fourth ventricle,

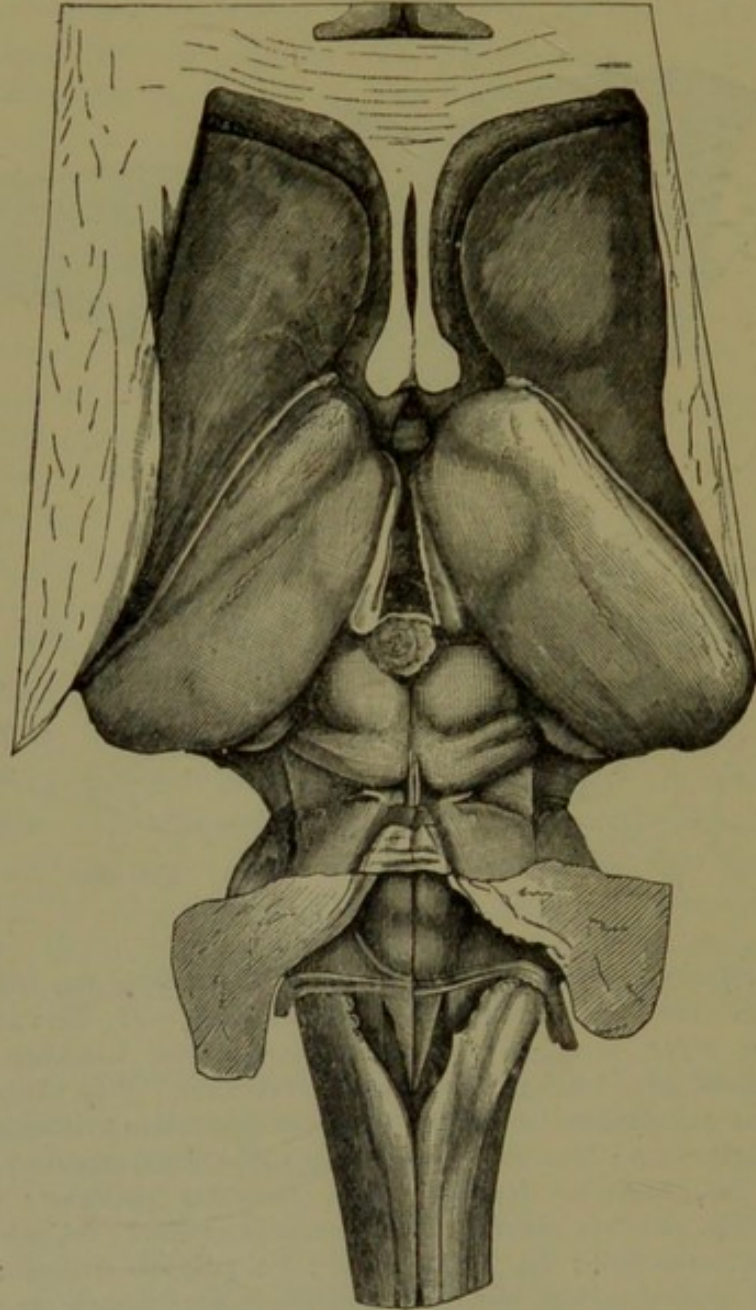
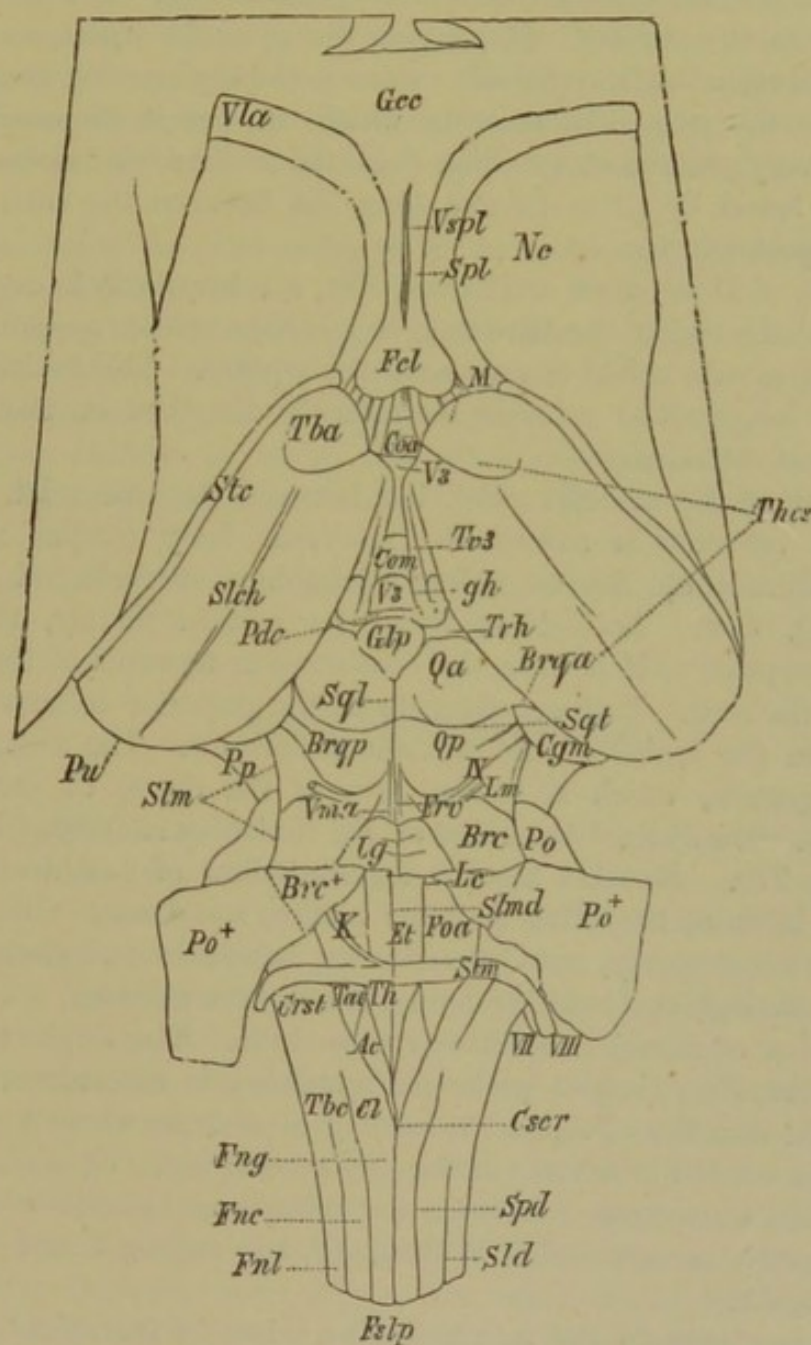


Fig. 12.—Hind-brain, mid-brain, and 'tween-brain from the dorsal surface (*natural size*). The greater part of the secondary fore-brain is removed by four sections, one horizontal, one frontal, and two sagittal. Most of the nerve-roots are cut away.—*IV*, N. trochlearis; *VII*, nervus facialis; *VIII*, nervus acusticus; *Ac*, ala cinerea; *Brc*, brachium cerebelli ad corp. quad. cut at *Brc+*; *Brqa*, brachium corp. quad. anterior; *Brqp*, brachium corp. quad. posterior; *Cgm*, corpus geniculatum mediale; *Cl*, clava; *Coa*, commissura anterior; *Com*, commissura mollis; *Crst*, corpus restiforme; *Cscr*, calamus scriptorius; *Et*, eminentia teres; *Fcl*, columnæ fornicis; *Fnc*, funiculus cuneatus; *Fng*, funiculus gracilis; *Fnl*, funiculus lateralis; *Foa*, fovea anterior; *Frv*, frenulum veli anterioris; *Fslp*, fissura longitud. posterior; *Gcc*, genu corporis callosi; *gh*, ganglion habenulæ; *Glp*, glandula pinealis; *K*, conductor sonorus *vel* tractus auditorius; *Lc*, locus cæruleus; *Lg*, lingula; *Lm*,



and the posterior columns diverge to the two sides (calamus scriptorius, *Cscr*), exposing the fourth ventricle.

In the proximal part of the medulla appears a sharply marked fissure more than 1 cm. long, the sulcus postolivaris *seu* retro-olivaris (figs. 10 and



lemniscus or fillet; *M*, situation of foramen of Monro; *Nc*, nucleus caudatus; *Pdc*, pedunculus conarii; *Po*, pons at *Po+* cut across; *Pp*, pedunculus cerebri; *Pu*, pulvinar; *Qa*, corp. quad. anteriora; *Qp*, corp. quad. posteriora; *Slch*, sulcus choroideus; *Sld*, sulcus lateralis dorsalis; *Slm*, sulcus longitudinalis mesencephali; *Slmd*, sulcus longitudinalis medianus ventriculi quarti; *Spd*, sulcus paramedianus dors.; *Spl*, septum pellucidum; *Sql*, sulcus corp. quadrig. longitudinalis; *Sqt*, sulcus corp. quad. transversus; *Stc*, stria cornea; *Stm*, striæ medullares acusticæ; *Tac*, trigonum acustici; *Tba*, tuberculum anterius; *Tbc*, tuberculum cuneatum; *Th*, trigonum hypoglossi; *Thos*, thalamus opticus; *Trh*, trigonum habenulæ; *Tr3*, tænia ventriculi tertii; *Vla*, anterior horn of lateral ventricle; *Vma*, velum medullare anterius; *Vspl*, ventriculus septi pellucidi.



11), *Spo*. It extends from the margin of the pons to the sulcus lat. vent. In most cases a vessel is found lying in it.

The swellings which these furrows throw into relief are not equally prominent in all brains. The anterior columns of the cord are pushed aside by the pointed extremities of the pyramids (fig. 10, *Py*) until they disappear from the surface. If, pressing the pyramids apart, we look into the fissura longitudinalis ventralis we see it thickly set with fibre-bundles, belonging to the pyramidal crossing, which traverse it diagonally caudalwards. A very prominent swelling, the inferior olive (eminencia olivaris), 6 to 7 mm. broad by 12 to 14 mm. long, lies between the sulci ventralis lateralis et postolivaris.

A bundle of fibres, fibræ arciformes, *Fba*, can invariably be seen arching round the hinder end of the olive and, to a certain extent, spreading over it. It is not, as a rule, raised much above the surface. The funiculi siliquæ are minute longitudinal columns occasionally described on the mesial or lateral side of the olive.

The part of the medulla which lies between the sulcus lat. dors. and the fourth ventricle is named the restiform body (corpus restiforme, inferior peduncle of the cerebellum, brachium cerebelli ad medullam oblongatam), *Crst*. Looked at from the surface merely, the corpus restiforme appears as if it were the continuation upwards of the posterior column of the cord. Both constituents of the posterior column swell out somewhat in the region of the calamus scriptorius. The swelling of the funiculus gracilis, which is known here as the clava, *Cl* (or posterior pyramid), is more distinct than that of the funiculus cuneatus (tuberculum cuneatum), *Tbc*. In most cases a vacant hollow of considerable length intervenes between the olive and the corpus restiforme. In the distal end of it is found a grey, rounded eminence, tuberculum cinereum Rolandi, *TcR*, only distinguishable in the brains of new-born children.

A number of nerves arise from the medulla. The origin of the first cervical nerve, *RacI*, is also prolonged upwards into this region. Between the pyramid and the olive, and extending almost the whole length of the latter, come out the root-fibres of the hypoglossus (fig. 10), *XII*. Between the olive and the corpus restiforme an uninterrupted series of roots take exit to join the n. accessorius Willisii, *XI*, the vagus, *X*, and the glossopharyngeal, *IX*.

The larger part of the n. accessorius arises in the spinal cord; the root-fibres which pass out through the lateral column extend as far downwards as the fifth pair of nerves. It is impossible to distinguish with certainty the upper roots of the n. accessorius which are attached to the medulla in the region of the olive from those of the vagus, or the vagus fibres from those of the glossopharyngeal. All one can do is to assign the more distal fibres to the accessorius, the more proximal to the glossopharyngeal. In the furrow between the pons and the pyramid, 2 mm. from the median line, the n. abducens arises in several bundles, quickly uniting together, which pass out in the transverse furrow between the pyramid and the pons.



Bundles of fibres, *striæ medullares*, *Stm* (fig. 12), take origin in the floor of the fourth ventricle, and, encircling the corpus restiforme, just before it sinks into the cerebellum, join with another bundle, *VIII* (fig. 10), which comes out from the corpus restiforme itself, to form the n. acusticus. A little swelling at the edge of the fourth ventricle, the tuberculum acusticum, corresponds to one of the centres from which the eighth nerve takes origin (its accessory nucleus). Mesially to the auditory nerve and rather close to its ventral side the facial nerve takes exit in a strong bundle. The description of the floor of the fourth ventricle will follow in another place.

Of the roof of the after-brain, so far as it concerns the fourth ventricle, I shall also speak elsewhere.

With regard to the development of the after-brain, I will only say here that in the human embryo the olives appear before the pyramids, being distinguishable as early as the third month.

The only animals in which the olives are noticeably prominent are apes and Cetacea, and even in the lower apes the prominence is very slight.

In no animal are the pyramids as large or as well-marked externally as in man.

## 2. THE HIND-BRAIN.

The pons, *Po*, comprises an immense tract of crossing fibres, measuring about 3 cm. from before backwards, and 4 cm. from side to side. At either side the pons constitutes a more rounded column, the middle cerebellar peduncle (brachium cerebelli ad pontem), fig. 12, *Po+*, which passes dorsally into the cerebellum. This closes the ring through which the columns of the hind-brain must pass on their road forwards.

The **cerebellum**, looked at from above (dorsally), presents a deep notch, incisura marsupialis, *Im*. On its ventral or under margin is a shallower, broader notch, incisura semilunaris, *Isl*. The former contains the process of the dura mater known as the falx cerebelli, while the latter is filled up with a portion of the mid-brain (*Mh*). On the dorsal surface a ridge extends from the one notch to the other, from which (as from the roof-tree of a house) the two surfaces of the cerebellum slope away. On either side of this ridge a shallow groove, sulcus longitudinalis superior cerebelli, *Sisp*, marks off the superior vermis, *Vrsp*, from the lateral lobes.

The dorsal surface of the cerebellum is completely covered in grey cortex-substance.

The ventral side of the cerebellum can only be seen by cutting through the massive columns which unite it with the other parts of the central nervous system. On this side the median part or vermis inferior (fig. 14), *Vrif*, is sharply cut off by deep furrows, sulci longitudinales inferiores (*Slif*), from the lateral hemisphere. The great lateral hemispheres arch over and



hide the vermis inferior, shutting it up in the vallecula. It can only be brought into view by pressing the hemispheres aside.

The anterior part of the vermis inferior does not reach into the incisura semilunaris. A layer of white substance extends brainwards in front of it, the velum medullare anterius or roof of the front part of the fourth ventricle; on this is borne a recurved part of the superior vermis. It follows from this that the superior vermis is much longer than the inferior. The ventral surface of the cerebellum is not entirely covered with grey matter.

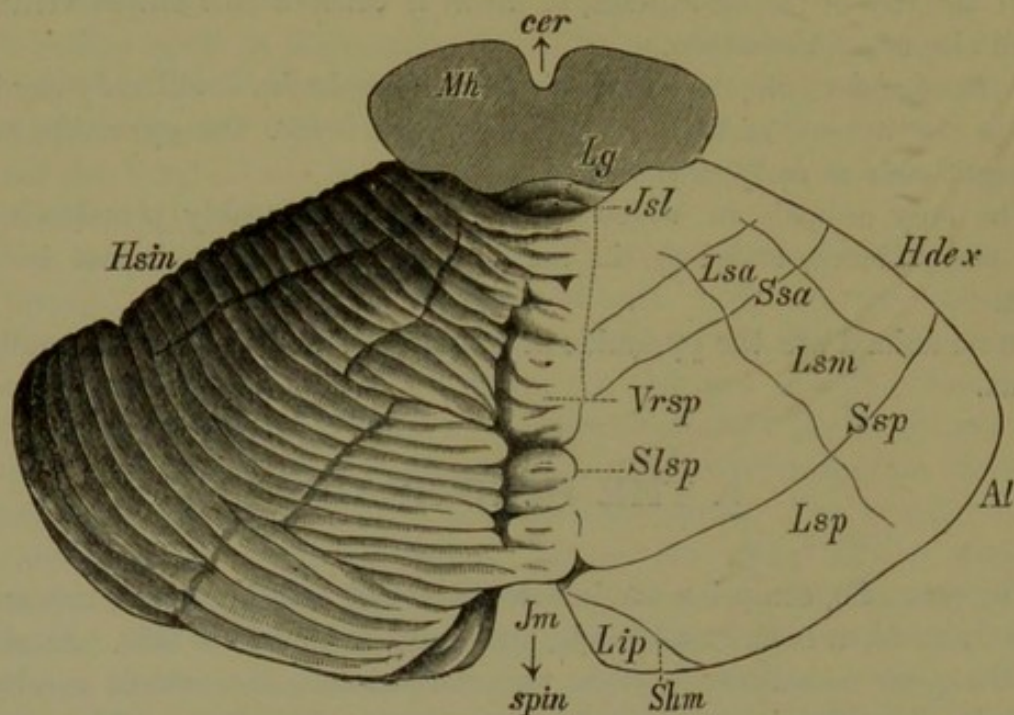


Fig. 13.—Cerebellum, dorsal view (*natural size*). The mid-brain is cut across behind the corpora quadrigemina at *Mh*.—*Al*, Lateral angle of hemisphere; *H*, hemispheres of cerebellum, *dextera et sinistra*; *Jm*, incisura marsupialis; *Jsl*, incisura semilunaris; *Lg*, lingula; *Lsa*, lobus superior anterior; *Lsm*, lobus superior medius; *Lsp*, lobus superior posterior; *Shm*, sulcus horizontalis magnus; *Ssa*, sulcus superior anterior; *Ssp*, sulcus superior posterior; *Vrsp*, vermis superior.

The surface of the cerebellum is broken up in a characteristic way by a large number of **furrows**. They are not, as a superficial examination would lead one to think, of anything like equal depth. If the cerebellum is cut at right angles to the direction which these furrows assume, it will be seen that some of them extend so much deeper than others as to make it possible to divide the organ into lobes (fig. 15).

There is no uniformity in the classification of these lobes and their nomenclature. The lobes are divided by secondary furrows into lobules, which again bear convolutions. The greatest fissure is the sulcus horizontalis magnus, *Shm*, which divides the cerebellum into an upper [in lower animals anterior] and lower [or posterior] part. This deepest and most constant of the fissures of the cerebellum originates at the middle peduncle, and extends around the cerebellum almost parallel to its border. At first it lies



a little on the under surface, near the incisura marsupialis, it then extends over the border, and for a short distance before its termination belongs to the upper surface (fig. 13).

The fissures on the upper surface are thickly set. They form arches parallel to the hinder border of the cerebellum and the incisura semilunaris, the centre of their curvature being situate in the region of the corpora quadrigemina. Two of these are fairly constant and important; they divide the upper surface of each hemisphere into three divisions. They are named sulci cerebelli superiores anterior, *Ssa*, et posterior, *Ssp*.

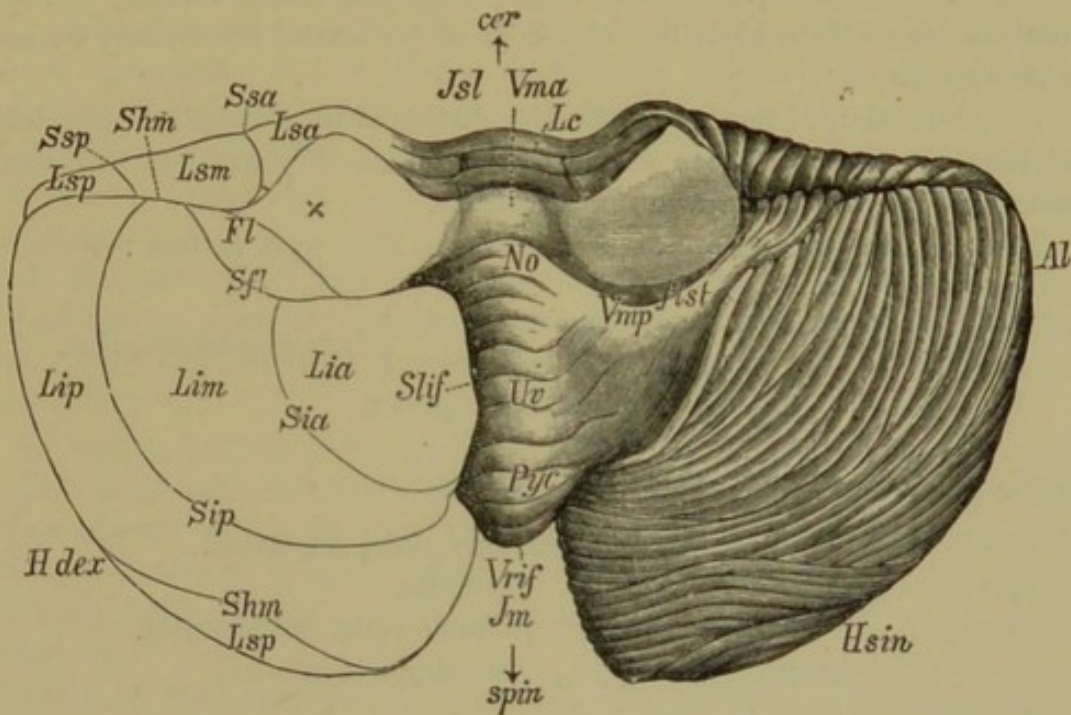


Fig. 14.—Cerebellum from the ventral side. *Nat. size.* The cerebellar peduncles are cut at *x*. The anterior lamina tectoria is cut away from its attachment to the mid-brain. The lobus anterior inferior is broken away from the left hemisphere.—*Al*, Angulus lateralis; *Fl*, flocculus; *Fst*, pedunculus flocculi; *Hdex*, right hemisphere; *Hsin*, left hemisphere; *Jm*, incisura marsupialis; *Jsl*, incisura semilunaris; *Lc*, lobulus centralis; *Lia*, lobus inferior ant.; *Lim*, lobus inf. med.; *Lip*, lobus inf. post.; *Lsa*, lobus sup. ant.; *Lsm*, lobus sup. med.; *Lsp*, lobus sup. post.; *No*, nodulus; *Pyc*, pyramid; *Sfl*, sulcus flocculi; *Shm*, sulcus horizontalis magnus; *Sia*, sulcus inf. ant.; *Sip*, sulcus inf. post.; *Slif*, sulcus longitudinalis inf.; *Ssa*, sulcus sup. ant.; *Ssp*, sulcus sup. post.; *Uv*, uvula; *Vma*, velum medullare anterius; *Vmp*, velum medullare posterius; *Vrif*, vermis inferior.

The anterior fissure (fig. 14) commences on the middle peduncle and crosses the vermis to join the fissure on the opposite side. The upper surface of the vermis is divided by it into two almost equal segments (fig. 13). The posterior fissure commences in the great horizontal sulcus, a little in front of the postero-external angle of the cerebellum. Crossing the upper surface it almost reaches the horizontal sulcus again at the spot where the latter passes on to the vermis, without, however, actually joining it.

The fissures on the under surface of the cerebellum present the same want of regularity. Two principal fissures are, however, again to be



recognised, sulci cerebelli inferiores anterior et posterior, *Sia* and *Sip*. Another short but deep fissure leaves the great horizontal fissure in a gentle curve directed backwards, and ends in the groove between the cerebellum and the medulla, sulcus flocculi, *Sfl*. The anterior inferior sulcus does not commence as does the posterior inferior in the great horizontal sulcus, but in the floccular sulcus.

The disposition of the sulci on the vermis is best seen in a median sagittal section (fig. 15). Both its superior and inferior surfaces are crossed by three chief fissures which are too short to need separate names. As a rule, no distinct furrow separates the upper from the under vermis; the continuation across the middle line of the great horizontal fissure may be used for this purpose.

The above-named fissures divide the surface of the cerebellum into lobes and lobules. On the under surface at any rate they are not sufficiently constant to allow of a uniform nomenclature.

**The hemispheres** are divided into—on the upper surface :—

Anterior lobe, <i>Lsa</i> , seu lunatus anterior,	} Lobus quadrangulus.
Middle „ <i>Lsm</i> , „ „ posterior,	
Posterior „ <i>Lsp</i> , „ semilunaris superior.	

On the under surface :—

Anterior lobe, <i>Lia</i> , seu amygdala, seu tonsil.	
Middle „ <i>Lim</i> , „	{ gracilis.
	{ cuneiformis, seu biventer.
Posterior „ <i>Lip</i> , „	semilunaris inferior.

The three upper as well as the two posterior lobes on the under surface have a pronounced semilunar form. Only the anterior lobe or tonsil, which pushes itself in towards the middle line, has a more complicated shape. The two tonsils from opposite sides meet in the middle line above the medulla oblongata, hiding the inferior vermis, and forming a close-fitting grooved cowl for its dorsal side. The floccular sulcus cuts off a small, but very conspicuous, lobe, the flocculus or lobus vagi, *Fl*, which occupies the commencement of the great horizontal fissure resting on the middle peduncle. Some small accessory lobules, which lie beside the flocculus on the middle peduncles, are known as accessory flocculi.

Proceeding from the front of the vermis backwards along its upper surface, and continuing our course along its under surface (fig. 15), we find :—

1. The lingula, *Lg*, a tiny tongue-shaped lobule, made up of from five to eight minute convolutions, lying on the velum medullare anterius, *Vma*. It generally presents a sagittal furrow in the middle line. Sometimes its under surface is free from the velum, in which case it also is marked by transverse convolutions. The lingula extends on either side in a little leaflet, the frenulum lingulæ, which represents an atrophied portion of the lateral hemisphere.



2. The central lobe, *Lc*, corresponds to a single division (the most anterior) of the medullary substance, and projects forwards until it touches the back of the corpora quadrigemina. To this piece of the vermis again belongs an inconspicuous portion of the hemisphere, the *ala lobi centralis*.

3. The upper lobe of the vermis (or monticulus) comprises by far the largest part of the vermis. It is again divided into two—(a) culmen (apex), *Cu*, reaching as far backwards as the union of the anterior superior sulci of the two sides, *Ssa*; (b) declive, *Dc*, reaching thence backwards to the posterior superior fissure (*Ssp*).

Both to the upper and the under vermis belong:

4. The posterior lobe of the vermis; divided again into (a) the little folium cacuminis, *Fcc*, a single convolution bounded by the posterior superior and the great horizontal sulci; (b) the tuber valvulæ, *Tv*.

5. The pyramis, *Pyc*, is the next section of the vermis, consisting of from five to eight folia. It attains to its greatest breadth behind the amygdalæ.

6. The part of the inferior vermis in front of the pyramis is narrow and shaped like a steep house-roof. It is called, on account of its situation with regard to the tonsils, the uvula, *Uv*; it presents six to ten free transverse folia.

7. Lastly, in front of the uvula projects a little knob, the nodulus, *No*.

[The importance of these names is somewhat diminished by the fact that, as can be seen in fig. 15, they do not exhaust the lobes of the vermis, and also by a doubt as to their morphological value. No serious attempt has yet been made to trace the lobation of the cerebellum throughout the vertebrata.]

An exact correspondence of furrows and convolutions in the two hemispheres is not to be looked for.

Anomalies of convolution, striking deviations from the ordinary course of the above-named furrows and convolutions of the cerebellum that is to say, occur very seldom. The peculiar formation known as *Lobus medianus cerebelli* deserves mention. In this anomalous formation the place of the parallel sulci longitudinales superiores is taken by two very marked sulci arising from the incisura marsupialis and diverging as they proceed forwards, so that the vermis superior assumes the shape of a triangle with its base to the front. It is also considerably larger than in normal brains. This abnormal development is said to be commonest in the brains of criminals and madmen (*Lombroso, Flesch*), but it occurs in others also.

The **medullary centre** of the cerebellum consists of two egg-shaped masses of white substance belonging to the hemispheres, and united together by the medullary substance of the vermis. The white substance is, in the main, a repetition in miniature of the whole cerebellum; but the portion belonging to the vermis is not relatively so large as the rest.

Portions of the medullary centre are prolonged into the lobes and lobules, dividing repeatedly, and occupying the centres of all the folia. A special description of these divisions of the medullary substance is, therefore, unnecessary. Those of the vermis, as they are represented in fig. 15,



may be mentioned. The central white substance of the vermis, called corpus trapezoides (a name which has given rise to mistakes), gives off two principal branches. One of these, the vertical branch, *Rv*, projects upwards into the monticulus. The other, or horizontal branch, *Rh*, is directed backwards into the central mass of the hinder lobes; quite near its origin this horizontal limb gives a considerable branch downwards into the pyramid. A less important branch passes in front of the vertical ramus into the central lobe, while another is continued in front of the horizontal one into the uvula. A still smaller branch enters the nodule, whilst the most minute of all forms the medullary substance of the lingula. The branches of the vermis taken together constitute, with their cortical covering, the arbor vitæ.

In connection with the cerebellum, although not really belonging to it, for it forms rather the embryonal roof of the fourth ventricle, the velum medullare posterius Tarini (*seu* valvula semilunaris), *Vmp*, must occupy our attention. To exhibit this structure it is necessary to cut off the medulla oblongata at the level of the hinder border of the pons, and then to break off the tonsils of the cerebellum. Fig. 14 shows the left velum

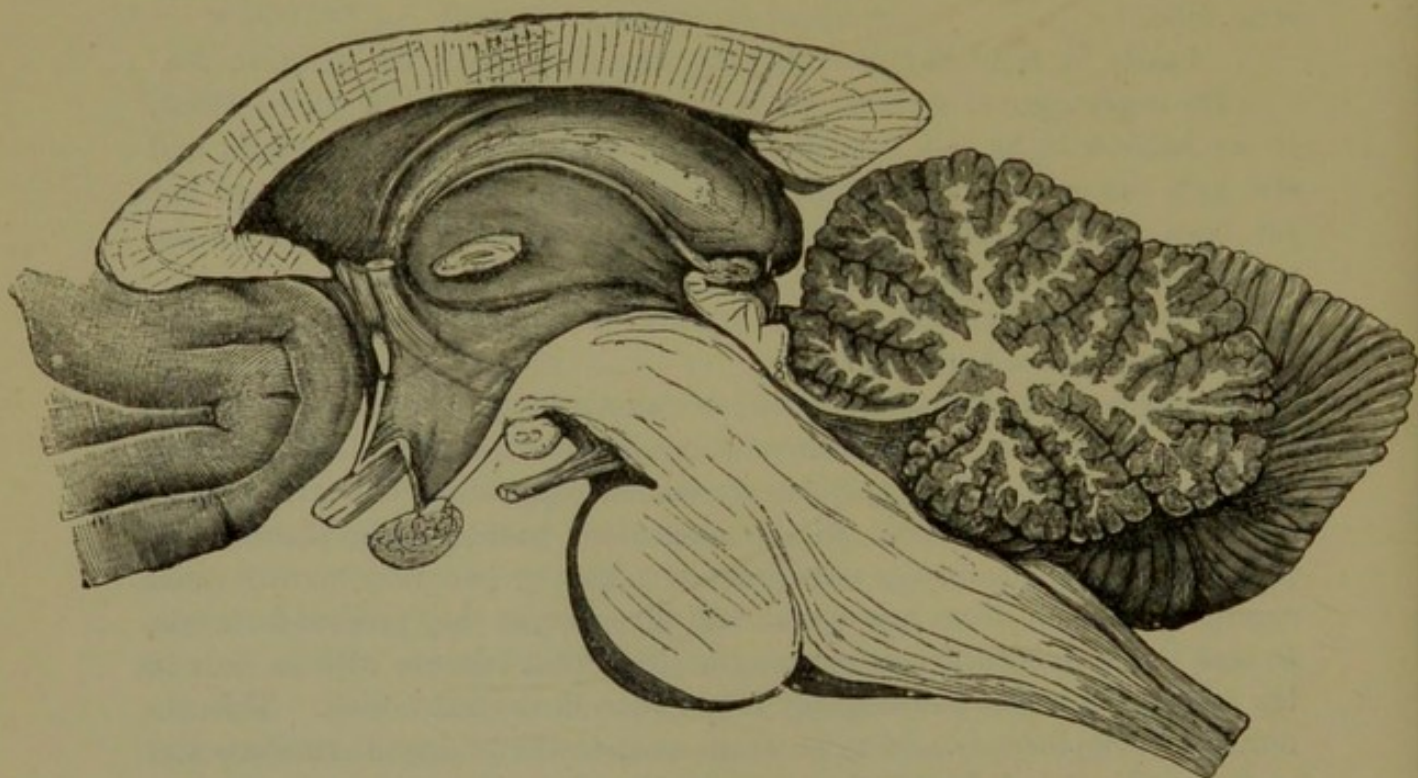


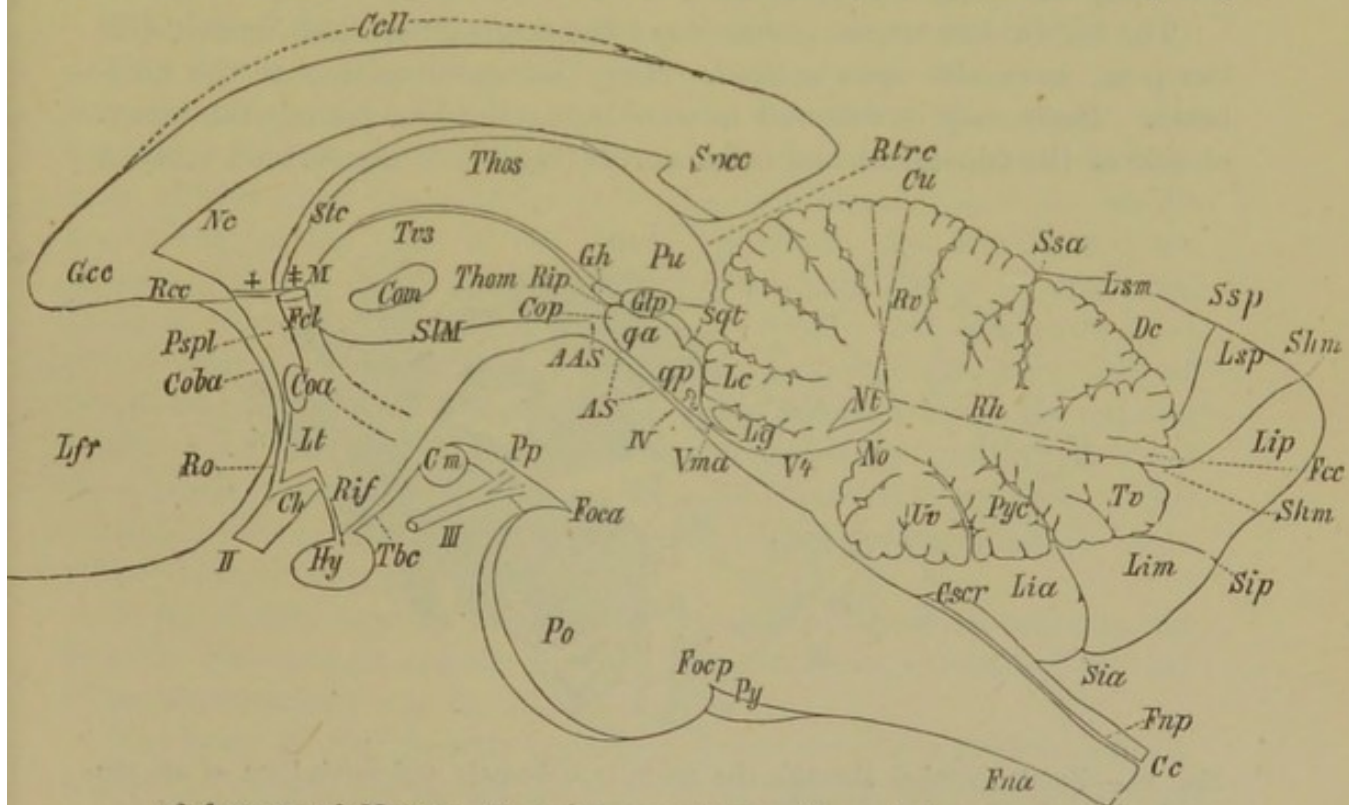
Fig. 15.—Sagittal section through the brain in the median line. *Right half. Nat. size.* Of the cortex of the cerebrum only a part of the frontal region is drawn.—*II*, Nervus opticus; *III*, nervus oculomotorius; *AAS*, aditus ad aquæductum Sylvii; *AS*, aquæductus Sylvii; *Cc*, canalis centralis; *Cell*, corpus callosum; *Ch*, chiasma nervorum opticorum; *Cm*, corpus mammillare; *Coa*, commissura anterior; *Coba*, commissura baseos alba; *Com*, commissura mollis; *Cop*, commissura posterior; *Cscr*, calamus scriptorius; *Cu*, culmen; *Dc*, declive; *Fcc*, folium cacuminis; *Fcl*, columna fornicis cut across at  $\pm$ ; *Fna*, funiculus ant. med. spinalis; *Fnp*, funiculus post. med. spin.; *Foca*, foramen cæcum ant.; *Focp*, foramen cæcum post.; *Gcc*, genu; *Gh*, ganglion habenulæ; *Glp*, glandula pinealis; *Hy*, hypophysis; *Lc*, lobulus centralis; *Lg*, lingula; *Lia*, lobus inf. ant.; *Lim*, lobus inf. med.; *Lip*, lobus inf. post.; *Lsm*, lobus sup. med.; *Lsp*, lobus sup. post.; *Lt*, lamina terminalis; *M*, situation



medullare posterius on the right-hand side of the picture. Each tonsil is now seen lying with its upper surface in a hemispherical depression, the floor of which is not formed by the substance of the cerebellum but by a delicate transparent membrane, which stretches from the uvula and nodule on either side as a semilunar leaflet attached along its posterior convex border to the cerebellum, but presenting a free concave border directed forwards. It is comparable in appearance to one of the semilunar aortic valves. Laterally the free edge is prolonged into a bundle of nerve-fibres, which can be followed as far as the flocculus, *Flst*; stalk of the flocculus.

Grey matter is also to be found in the medullary centre of the cerebellum. It can be shown by cutting the cerebellum horizontally, the section following the sulcus horizontalis magnus, or by making at right angles to this sulcus a section inclining obliquely outwards and backwards from the incisura semilunaris. In either case the corpus dentatum cerebelli, *Ndt*, appears as a narrow grey zigzag band.

The corpus dentatum, *Ndt*, fig. 16 (*seu* nucleus dentatus *seu* fimbriatus *seu* lenticulatus, corpus ciliare *seu* rhomboideum), is a puckered up bag



of foramen of Monro; *Nc*, nucleus caudatus; *No*, nodulus; *Nt*, nucleus tecti; *Po*, pons; *Pp*, pes pedunculi; *Pspl*, pedunculus septi pellucidi cut at +; *Pu*, pulvinar thalami; *Pyc*, pyramis cerebelli; *Qa*, corpus quadrigeminum anterius; *Qp*, corpus quadrigeminum posterius; *Rcc*, rostrum; *Rh*, ramus medullaris horizontalis; *Rif*, infundibulum; *Rip*, recessus infrapinealis; *Ro*, recessus opticus; *Rtrc*, rima transversa cerebri; *Rv*, ramus medullaris verticalis; *Shm*, sulcus horizontalis magnus; *Sia*, sulcus inf. ant.; *Sip*, sulcus inf. post.; *SLM*, sulcus Monroi; *Spec*, splenium; *Sqt*, sulcus corp. quad. transversus; *Ssa*, sulcus sup. ant.; *Ssp*, sulcus sup. post.; *Stc*, stria cornea; *Tbc*, tuber cinereum; *Thom*, thalamus opticus, mesial surface; *Thos*, thalamus opticus, upper surface; *Tv*, tuber valvulae; *Tv3*, tænia ventriculi tertii; *Uv*, uvula; *Vma*, velum medullare ant.; *V4*, fourth ventricle.



of grey substance, the open mouth of which looks a little mesially and ventrally. It lies in the mesial half of the hemisphere, and so close to the ventricle that it is only separated from it by a thin layer of white substance. Its longest antero-posterior diameter (converging somewhat with that of the opposite side) is about 2 cm. The corpus dentatum is not seen in its greatest extension in a frontal section.

Another not well-defined, light grey or brownish mass, oval in shape, appears between the two corpora dentata in a frontal section. This is *Stilling's* roof-nucleus, *Nt* (nucleus tecti seu fastigii, substantia ferruginea superior). Between the corpus dentatum and the nucleus of the roof are some little scattered clumps of grey matter which *Stilling* names the nuclei emboliformis et globosus. *Meynert* calls them both the nuclei subdentati (gezackte nebenkerne). In fig. 16, taken from the brain of the monkey, these nuclei are not visible.

The medullary substance of the cerebellum is supplied by large white bundles which stream into this organ on three sides. One of these bundles, the corpus restiforme, which skirts the margin of the fourth ventricle, has been already noticed, *Crst*.

The middle and largest peduncles of the cerebellum, which unite it with the pons, have also been noticed. They belong altogether to the hind-brain. *Henle* may be followed in considering the line joining the points of exit of the trigeminal and facial nerves (fig. 10) as the division between

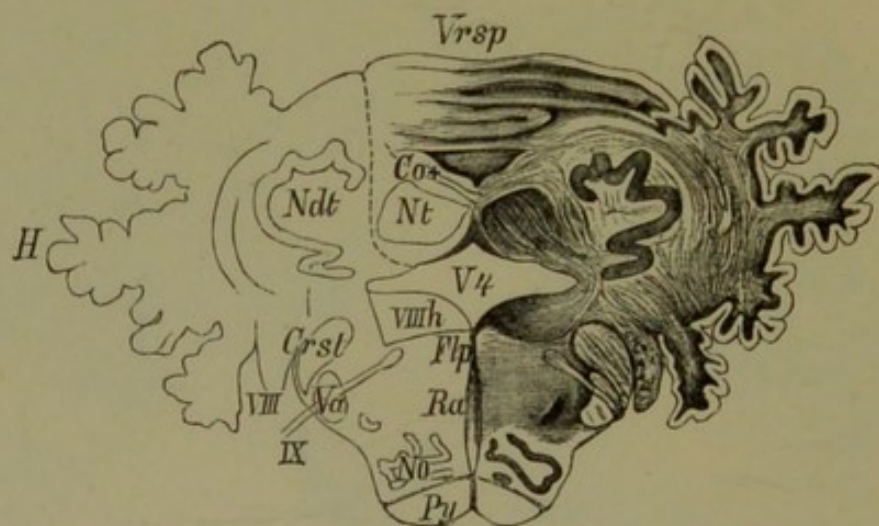


Fig. 16.—Frontal section through the medulla oblongata and cerebellum of an ape (*twice natural size*).—VIII, Nervus acusticus; VIIIh, chief auditory nucleus; IX, nervus glossopharyngeus; Co+, superior commissure (and decussation); Crst, corpus restiforme; Flp, fasciculus longitudinalis post.; H, hemisphere of cerebellum; Ndt, nucleus dentatus; No, nucleus olivaris; Nt, nucleus tecti; Py, anterior pyramid of the medulla; Ra, raphe; V4, ventriculus quartus; Va, ascending root of trigeminus; Vrsp, vermis superior.

the middle peduncle and the pons proper. The greater number of fibres in the pons are directed transversely (*Foville* compares their appearance as seen from the mid-ventral line to a head of hair parted in the middle); a broad band of fibres is, however, conspicuous in the anterior half of the



pons, which, starting in the usual direction, subsequently inclines backwards and outwards over the surface of the others towards the point of exit of the facial nerve. It is called the fasciculus obliquus (ruban fibreux oblique of *Foville*), fig. 10, *Fob*.

A bundle of fibres, the ponticulus, *Pol*, is usually to be seen along the hinder border of the pons, spreading over the pyramid.

The third pair of cerebellar peduncles, which have not yet been mentioned, pass from this organ towards the great brain converging in this direction much in the same way as the posterior peduncles converge spine-wards. They and the posterior peduncles together bound a rhomboidal space; sinus rhomboidalis (or fourth ventricle). They look as if they went to the corpora quadrigemina, and hence have been named by mistake the processus cerebelli ad corpora quadrigemina. They are also named the brachia conjunctiva (*seu* conjunctoria, processus cerebelli ad cerebrum); compare figs. 11 and 17, *Brc*.

Between the mesial edges of the anterior peduncles lies a thin tongue-shaped membrane with its point turned brainwards, the velum medullare anterius, *Vma*, already described; on it lies the lingula, *Lg*.

The lateral borders of the anterior peduncles are not really visible, for as they converge forwards to slip under the posterior tubercles of the corpora quadrigemina they are overlapped, even from the moment that they leave the pons, by two other white tracts, the lemnisci, which converge more quickly than the anterior peduncles, and almost reach the middle line in front of the point of the velum medullare. The lemniscus (fillet, laqueus, ruban de Reil), *Lm*, has a triangular form (hence its occasional name of trigonum lemnisci), and is usually divided into two parts by a shallow furrow, which also runs brainwards and mesially. An isolated bundle can almost always be seen lying in the furrow between the anterior border of the pons and the superior cerebellar peduncles; passing on round the cerebral peduncles it sinks at last into the fissure between them. This bundle, the tænia pontis, *Tpo* (fig. 11), can sometimes be lifted up for a considerable distance as a free cord.

It has already been mentioned that the great fifth nerve takes its exit from the pons near its anterior border. The motor-root is attached in front of the larger sensory one, fig. 10, *Vm* and *Vs*.

The **floor of the fourth ventricle** (sinus *sive* fossa rhomboidalis) is exposed by cutting the cerebellum from all its connections with the rest of the brain. It is longest in its antero-posterior diameter (about 3 cm.). Its greatest breadth (about 2 cm.) is in the line connecting the attachments of the auditory nerves. The margins of the sinus rhomboidalis are formed in front by the superior cerebellar peduncles, and by the corpora restiformia behind.

Of the two diagonals of the sinus, the longitudinal is marked by a conspicuous fissure (sulcus medianus longitudinalis sinus rhomboidalis), *Slmd*, while transverse bundles of fibres (striæ medullares, *seu* acusticæ, *seu* chordæ acusticæ, barbe de Piccolomini), *Stm*, starting in the middle line, pass outwards to encircle the corpora restiformia, and join the auditory



nerve. These striæ acusticæ are subject to great individual variations. They may in exceptional cases be absent on one side, or even on both sides. Occasionally they are very strongly developed. Sometimes individual bundles cross over one another during their course. Bundles lying quite free, not fused with the floor, may also be met with. Besides the usual tracts which cross the corpus restiforme to join the auditory nerve, other bundles of white fibres are also generally to be met with in the floor of the fourth ventricle, such a bundle [the conductor sonorus seu tractus acusticus], the 'Klangstab' of *Bergmann*, fig. 23, *K*, is often to be found originating in the median fissure, near the striæ medullares, and passing obliquely outwards and forwards towards the anterior cerebellar peduncles. It is often more strongly developed on the left side. The angle which it forms with the middle line varies considerably. It frequently bridges over some of the striæ medullares at its origin. Sometimes it runs brainwards by the side of the sulcus longitudinalis medianus and almost parallel to it. Its thickness, too, varies greatly in individual brains, and it often consists of several separate bundles of different course.

Three divisions can be recognised in the posterior half of the sinus rhomboidalis on either side of the middle line. The most mesial of these forms a right-angled triangle with the right angle bounded on one side by the median fissure, on the other by the striæ acusticæ, the apex lying near the calamus scriptorius. This triangular region is covered with white substance; it corresponds in the main with the nucleus of the hypoglossal nerve, and may, therefore, be named the trigonum hypoglossi, *Th*.

Laterally to this triangle lies another with its apex against the striæ acusticæ. Its surface is a little depressed below the rest of the floor of the fourth ventricle and is grey in colour. Since it corresponds very closely to the nuclei of the vagus (and glossopharyngeus) it may be called the trigonum vagi (it is more often named ala cinerea, hence the lettering *Ac*). The lateral portion of the posterior half of the floor of the fourth ventricle is raised above the general surface. It extends beyond the striæ acusticæ brainwards, and there attains its greatest development. It is termed the tuberculum acusticum [a well-marked swelling in the child's medulla], since it corresponds to a group of nerve-cells which many regard as the nucleus of this nerve.

On the proximal [anterior] half of the floor of the fourth ventricle is a cylindrical eminence, about 4 mm. broad, lying on either side the middle line. Commencing as the continuation upwards of the trigonum hypoglossi, it extends to the front of the fourth ventricle beneath the corpora quadrigemina; at their upper part, owing to the drawing together of the superior cerebellar peduncles, these eminences, *Et*, eminentiæ teretes (wrongly called funiculi teretes), are somewhat contracted.

Laterally to the eminentia teres a depressed spot is visible, the fovea anterior, *Foa*, distinguished, as a rule, by the presence of a fairly large superficial vein. I have already pointed out that the area acustica extends into the anterior part of the fourth ventricle.



Lastly, in the front of the floor, near the lateral angle, is to be noticed a dark brown or bluish space, stretching forwards for from 4 to 6 mm. as far as the corpora quadrigemina, locus cœruleus, *Lc.* Its colour, which is not always visible until the surface has been scratched, is due to a strongly pigmented group of nerve-cells, substantia ferruginea, which shows through the upper layer of the medulla.

At its proximal extremity the ventricle has a breadth of 3 mm. Beneath the corpora quadrigemina it sinks into the aquæductus Sylvii, *Qp.*

The cerebellum cannot be looked upon as a portion of the roof of the hind-brain. It is a secondary formation which grows later from the two sides and arches over the fourth ventricle. The following structures cover in the ventricle:—

1. The front is covered by the velum medullare anterius.
2. The middle part by the vela medullaria posteriora.

3. The roof of the hinder part of the ventricle is formed by a thin vascular membrane, reduced for the greater part of its extent to a triangular layer of epithelium and pia mater, tela choroidea inferior ventriculi quarti. This is continuous in front with the vela posteriora. It is shown when the back of the cerebellum is lifted up from the medulla oblongata. Some other small and unimportant developments (little plates of white matter) are found in this part of the ventricle, namely, the obex (often absent) which fills in the angle between the diverging funiculi graciles and the tæniæ ventriculi quarti, *Alp* (ligulæ, alæ pontis, ponticulus), fig. 11, which skirt the outer margin of the ventricle as far forwards as the striæ acusticæ. These little plates of white matter are very delicate and easily torn off with the membranous roof of the ventricle with which they are intimately connected; in fig. 12 they are only partly visible. The base of the triangular membrane corresponds to the vermis, and fuses with its pia mater.

A peculiar shaggy plexus of vessels, the plexus choroideus cerebelli medialis, hangs to the under surface of the tela choroidea on either side of the middle line. The depending fringes commence at the calamus scriptorius, and take a sagittal direction as far forwards as the back of the velum medullare posterius. Here they turn outwards, and lying on the under side of the cerebellum, run along the stalks of the flocculi to meet the auditory nerves, where they form a somewhat larger coil, the plexus choroideus cerebelli lateralis (ala, plexus nervi vagi). In the part of the roof of the ventricle, which is thinned out as the tela choroidea, three gaps are formed during the course of development, the only communications, perhaps, between the brain-ventricles and the pericerebral space. Between the two plexus choroidei mediales, and just in front of the calamus scriptorius, a large hole is pierced in the roof, easy to demonstrate although at one time its existence was much doubted, the foramen Magendii (apertura inferior ventriculi quarti, orifice commun des cavités de l'encéphale). We often find the tela choroidea pierced in this place by several irregular holes instead of a single opening. In the embryo the foramen Magendii is said to be clearly distinguishable at the end of the fifth month. There are also always to be found, as *Key* and *Retzius* have proved, two



other openings, which lie at the lateral angles (*recessus laterales ventriculi quarti*) of the *tela choroidea*, just where the *plexus choroideus lateralis* comes out, *aperturæ laterales ventriculi quarti*. According to *Merkel* and *Mierzejewsky*, communications between the lateral ventricles of the great brain and the surface are also to be found in the form of elongated clefts above the *gyri hippocampi*. It is probable, however, that all such openings into the lateral ventricle are artificially produced.

To form an idea of the development of the cerebellum we must picture it as a thickening of the proximal anterior part of the hind-brain, taking in the first instance the shape of two lateral swellings, which grow together at a later period. The hinder segment, on the other hand, the true roof of the fourth ventricle, *membrana obturatoria ventriculi quarti*, becomes thin in the middle portion. This thinner part, which afterwards becomes the *tela choroidea posterior*, is pushed inwards towards the brain cavity by the growth of the *pia mater*, and doubled again and again to form the epithelium of the *plexus choroidei posteriores*. The peripheral parts of the *membrana obturatoria*, though much reduced in thickness, retain the form of platelets of white matter. The *velum medullare* is the only one of them that attains any considerable size. The *obex* and the *ligula* also originate in this manner.

In no mammal are the hemispheres of the cerebellum as highly developed as in Man, and consequently as we descend in the scale we find the *vermis* more and more preponderant. The lobation also presents great variations of detail. As the hemispheres decrease the *pons* dwindles. In most mammalia it stops short of the point of exit of the *nervus abducens* (see fig. 10), leaving a larger part of the brainward surface of the pyramids uncovered, and exposing a broad band of transverse fibres, the *corpus trapezoides*, which lies by their side.

In birds the hemispheres of the cerebellum are reduced to an inconsiderable appendage; in amphibia, fishes, and reptiles they are altogether lacking. In amphibia the *vermis*, too, is no more than a narrow transverse band, while in many fishes (several cartilaginous varieties, for example) the hind-brain not only shows very considerable development, but is marked by a number of furrows. In birds we find a tapering dorsal process of the fourth ventricle (*ventriculus cerebelli*) penetrating the substance of the cerebellum to a considerable depth.

The *foramen Magendii* occurs in many animals (*e.g.*, the dog, cat, ox), in others (*e.g.*, the horse) it is lacking. The *aperturæ laterales*, on the other hand, are said to be more highly developed in the animal last named than in the others.



### 3. THE MID-BRAIN.

Proceeding forwards we reach the mid-brain, or region in which the corpora quadrigemina are included. In connection with this region it will be necessary to describe structures which, although they belong properly speaking to the 'tween-brain, press themselves backwards into the mid-brain region.

The mid-brain is not more than a centimeter in length, and is divided by a furrow, the sulcus lateralis mesencephali, *Slm* (figs. 11 and 17), into two easily distinguishable parts; the ventral (basal) and dorsal portions of the mid-brain.

The sulcus lateralis is seen whether the brain-stem is looked at from above or from the side. It commences at the front of the pons and bounds the structure already described under the name of fillet.

The great **cerebral peduncle** (pes pedunculi cerebri), *Pp* (figs. 10, 11, and 12), lies on the ventral side of this furrow, and projects, laterally, somewhat beyond it. As it comes out from the pons it has a breadth of 12 to 20 mm., which is increased during its short superficial course. Passing beneath the optic tract, *TII*, it disappears from view in the interior of the great brain. It consists of bundles of fibres visible as separate bundles from the surface, not following its main direction, but giving it the appearance of a twisted cord. Those which are most mesially placed as it leaves the pons pass so abruptly to the outer side that they have an almost transverse course. These are the fibres, *LmP*, from the fillet to the peduncle, faisceau en escarpe, so called for reasons which will be presently explained. Each peduncle runs not straight forwards, but diverging from its fellow at an angle of 70° to 80°; a triangular space is thus left between the two, trigonum intercrurale, *Tric* (fossa interpeduncularis, *seu* Tarini [interpeduncular space]).

A deep furrow, from which the fibres of the oculomotor nerve emerge (sulcus oculomotorius), *SlIII*, marks the boundary between the pes pedunculi and the trigonum intercrurale. In the mid-line of the fossa is another well-marked furrow, sulcus substantiæ perforatæ posterioris, *Slpp*. The medial portion of the fossa, broad in front and pointed behind, constitutes the floor of the third ventricle. It is pierced by numerous blood-vessels, and hence is termed the substantia perforata posterior, *Sbpp*. The perforated space is bounded on either side by elongated swellings which really belong to the dorsal portion (the tegment) of the peduncle. They can only be seen when the peduncles are pushed aside, and hence are not visible in fig. 10.

The part of the mid-brain lying dorsally to the lateral sulcus presents two rounded swellings, the corpora quadrigemina (or in submammalian classes, bigemina), *Qa* and *Qp*. A median fissure, sulcus corporum quadrigeminae longitudinalis *seu* sagittalis, *SqL*, rising abruptly from the velum medullare, and opening out in front into a little shallow



triangular fossa, lodges the pineal gland, *Glp*, and separates the tubercles of the corpora quadrigemina of one side from those of the other. The triangular fossa, just mentioned (trigonum subpineale), often presents a slight elevation in the centre (colliculus subpinealis of *Schwalbe*). At the back, where it sinks on to the velum medullare, the fissure is bounded on either side by a little ridge of white substance (sometimes the two ridges are fused together), frenulum veli medullaris antici, *Frv*.

A transverse sulcus, sulcus corp. quad. transversus (*seu* frontalis), *Sqt*, crosses the median fissure at right angles, dividing the anterior pair of tubercles from the posterior. It is shallowest near the middle line.

The anterior tubercles, *Qa*, measure in the sagittal direction 8 mm., in the frontal direction 12 mm. The posterior tubercles, *Qp*, measure 6 mm. by 8 mm. The latter are distinguished by the abruptness of their posterior surfaces.

From each of the corpora quadrigemina a well-marked white bundle passes ventrally, laterally, and brainwards. These are the peduncles of the corpora quadrigemina (brachia conjunctiva). On each side the two brachia are separated by a continuation of the transverse furrow, which might well be called in this part of its course the sulcus interbrachialis.

The posterior brachium is soon divided into two by a shallow furrow. The posterior of these two divisions disappears in the sulcus lateralis mesencephali, near the fibres of the pes pedunculi. The anterior joins a spindle-shaped elevation of about 1 cm. in length, the internal geniculate body, *Cgm* (ganglion *seu* corpus geniculatum mediale *seu* internum), which is squeezed into the sulcus interbrachialis. It must be looked upon as a part of the 'tween-brain.

The anterior brachium, *Brqa*, a rather short bundle, almost lateral in direction, continues its course, covered by the overhanging optic thalamus, almost to the optic tract. It is broadest where it comes out from the anterior tubercle, but loses a considerable portion of its substance beneath the lateral geniculate body.

A thin nerve tract, which is very visible in many animals but rarely distinctly seen in Man, proceeds from in front of the anterior tubercles downwards, outwards, and backwards across the brachia, and then on across the pedunculus cerebri, tractus peduncularis transversus, fig. 11, *Tpt*. Its termination is never distinctly seen.

When the mid-brain is cut across at right angles to its long axis through the anterior corpora quadrigemina (fig. 17), the proximal continuation of the fourth ventricle, which leads to the ventricles of the cerebrum, aquæductus Sylvii, is to be seen in the middle line. In the substance of this part of the brain-stem several strata are distinguishable:—

1. The region of the corpora quadrigemina is limited by a line drawn transversely through the aqueduct, *Q*.

2. A region of mixed grey and white substance, the tegment, *Tg*.

3. A stratum which is at once distinguished by its colour, due to



the intensely black pigmentation of the cells of which it is composed, stratum nigrum, *Ss* (substantia nigra Soemmeringi, stratum intermedium).

4. Lastly, the lowest portion of the picture is occupied by the white semilunar section of the pes pedunculi or crusta, *Pp*.

The attachment of the oculomotor nerve, fig. 10, *III*, has been already mentioned. Most of it comes out of the sulcus oculomotorius; detached bundles, however, pierce the mesial surface of the crusta. Not infrequently a detached portion of the nerve, isolated from the main bundle by a blood-vessel, takes exit from the peduncle considerably further outwards, *III'*.

The trochlear nerve, figs. 11 and 12, *IV*, arises as a thin thread, or in some cases as two separate roots, from the lateral angle of the velum medullare. It lies usually in the furrow between the posterior tubercles of the corpora quadrigemina and the superior cerebellar peduncles.

In the early stages of development the mid-brain forms a comparatively large part of the whole, but its growth does not keep pace with

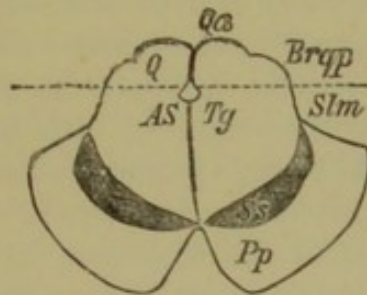


Fig. 17.—Transverse section through the anterior corpora quadrigemina (semi-diagrammatic).—*AS*, Aquæduetus Sylvii; *Brqp*, brachium posterius corporum quadr.; *Pp*, pes pedunculi; *Q*, region of the corpora quadrigemina; *Qa*, anterior corpora quadrigemina; *Ssm*, sulcus lateralis mesencephali; *SS*, substantia nigra Soemmeringi; *Tg*, tegmentum.

that of the rest of the brain, and in most mammalia the hemispheres of the cerebrum exceed it in size. The corpora quadrigemina first appear as a single rounded eminence. The longitudinal and transverse furrows are not developed until the fifth or sixth month of foetal life.

In most mammals the corpora quadrigemina are larger in proportion than in Man, the posterior corpora being the larger in beasts of prey, and the anterior in other mammals. In the ornithorhynchus only two corpora quadrigemina are said to be discoverable, and the same holds good of the lower vertebrates. In studying the exterior conformation of the brain in other vertebrate classes, excluding a few exceptions, we find a single spherical swelling on either hand, which is sometimes of very considerable size. In birds this swelling is thrust so far to the side that it extends to the base of the brain. The tractus opticus rises in these swellings; hence this part of the mid-brain is commonly called the lobus opticus.

But the posterior corpora quadrigemina are not entirely absent in lower vertebrates. In all we find a well-defined grey nerve-nucleus lying in the posterior or caudal part of the mid-brain. This it is which in



most mammalia becomes independent, and forms the posterior corpora quadrigemina.

#### 4. THE 'TWEEN-BRAIN.

In the fully-developed brain it is very difficult to fix the boundaries between this portion and the parts in front of and behind it, namely, the secondary fore-brain and the mid-brain.

The most important structures which it includes are the optic thalami, *Tho*, with the two corpora geniculata, *Cgl* and *Cgm*, the optic tracts, *TII*, and the corpora mammillaria, *Com* (figs. 10, 11, and 12).

One part of the optic thalamus, the pulvinar, *Pu*, has already been shown to press backwards against the corpora quadrigemina. If all the rest of the great brain which lies superficial to the thalami is cut away so that these are left uncovered, a view into the ventricles of the great brain is obtained. We will content ourselves, in the first place, with a description of the external appearances of the parts included in the 'tween-brain, reserving the study of their intimate structure until sections through the whole of the great brain are under discussion.

The OPTIC THALAMUS (*couche optique*), fig. 12, is a large oval body which lies upon the pedunculus cerebri, with its long axis inclined forwards and inwards. Its lateral portion, which is continued into the optic tract, arches outwards over the peduncle towards the base of the brain. The upper surface of the thalamus, *Thos*, appears white owing to a thin covering of fibres (*stratum zonale*), while its mesial surface is grey. The two are separated by an angular border.

The fairly flat mesial surfaces (fig. 15) of the two thalami are very near together, and at one part are actually fused in the middle line forming the [soft, grey, or] middle commissure, *Com* (*commissura mollis, seu media, seu grisea, seu trabecula cinerea*). It is a short band, usually flattened from above downwards, and easily broken. This commissure is not seldom completely wanting (*Ferraz de Macedo* estimates the proportion of cases in which this occurs at 20 per cent.). In some cases, on the other hand, it is double. In hydrocephalous distension of the ventricle, it may be drawn out to a considerable length (17 mm.—*Anton*).

The cavity of the 'tween-brain is named the middle or third ventricle, *V3*. The aqueduct of Sylvius opens out on reaching its oblique posterior wall into the *aditus ad aquæductum Sylvii*, fig. 15, *AAS*. From this a fissure runs along the middle of the posterior wall and floor of the ventricle. In the floor it opens out into a funnel-shaped depression, *recessus infundibuli*, *Rif*. This recess produces a grey conical swelling on the surface of the basis cerebri projecting behind the optic chiasm, *tuber cinereum* (fig. 10), *Tbc*. To the point of the infundibulum, *If*, hangs an ellipsoidal body, the hypophysis cerebri [pituitary body], *Hy*.

The white upper surface of the thalamus is bounded laterally by a furrow (fig. 19), which contains a large vein, as well as a thickened ridge of ependyma. At the bottom of the furrow there lies also a bundle of fibres.



Thickened ependyma and fibres together make the stria cornea, *Stc* (stria terminalis), figs. 15 and 18. The furrow begins at the front of the thalamus, runs outwards and backwards, and can be followed into the inferior horn of the lateral ventricle.

In addition to the general rounding of its upper surface the optic thalamus presents certain minor elevations (fig. 12). A distinct rounded elevation, about as large as a bean, constitutes its anterior end, tuberculum anterius, *Tba*. A shallow furrow, sulcus choroideus, *Slch*, starts at the back of this tubercle, and divides the rest of the surface into a mesial and a lateral portion. The back of the thalamus is elevated into the considerable rounded pulvinar, *Pu*. Beyond this the thalamus bends downwards and outwards, and narrows into a swelling, somewhat smaller than a bean, corpus geniculatum laterale (*seu* externum), in which the optic tract terminates. The optic tract encircles the peduncle, and meets on the basis cerebri with the tract of the opposite side in the chiasma nervorum opti-corum, *Ch*. The lateral corpus geniculatum does not lie immediately on the peduncle, for the mesial portion of the optic tract, which is directed towards the mesial geniculate body, insinuates itself between the two. A white tract, which unites the two geniculate bodies together, and is best seen in the new-born child, is named by *Rauber* ansa intergenicularis.

The boundary between the upper and mesial surfaces of the thalamus is rendered more evident by a ledge of white matter (stria medullaris thalami, habenula) which is generally continued into a plate of gelatinous substance projecting towards the middle line, tænia thalami (t. ventriculi tertii) figs. 12 and 15, *Tv3*. This overhanging ledge swells just in front of the trigonum subpineale into a club-shaped body, the ganglion habenulæ, *Gh*. Between this and the back of the thalamus lies a small triangular region, the trigonum habenulæ, *Trh*. Provided the membranes of the brain have not been dragged off roughly, a little conical body, the glandula pinealis (conarium), *Glp*, is seen lying in the horizontal fissure between the corpora quadrigemina. It is 8 to 12 mm. long. Short peduncles pass from the anterior end of the pineal gland, which forms part of the posterior wall of the third ventricle, to the ganglion habenulæ on either side, pedunculi conarii, commissura habenularum, *Pdc*. The posterior part of the third ventricle presents a little pit beneath the pineal body, recessus infra-pinealis (ventriculus conarii), *Rip* (fig. 15).

Below this a well-formed tract of white matter, visible when the pineal gland has been removed, crosses above the anterior opening of the aqueduct of Sylvius, the posterior commissure, fig. 15, *Cop*. It bounds the trigonum subpineale in front.

We are already acquainted with most of the structures which are found on the ventral surface of the 'tween-brain. They all belong to the regio subthalamica (hypothalamus). First, though properly belonging to the fore-brain, comes the optic chiasm, *Ch* (fig. 10), with the tuber cinereum, *Tbc*, with infundibulum and hypophysis in the angle made by the posterior edges of the optic tracts. Behind this again lie two white rounded eminences about the size of peas, corpora mammillaria (*seu* candicantia),



*Cm.* They form the proper anterior border of the trigonum interpedunculare.

Certain morphological relations of the interior of the thalamus opticus will, as already remarked, be better understood when we come to treat of preparations of the fore-brain.

To form an idea of the way in which the 'tween-brain develops from the primary fore-brain we must picture it, in the first instance, as a thickening of the primary anterior vesicle in its lateral parts; this is the rudiment of the thalamus opticus and the regio subthalamica.

The roof of the 'tween-brain consists almost throughout of a single layer of cells. Like that of the fourth ventricle, it is pushed into the brain-cavity by the pressure of the vascular pia mater, and forms the tela and plexus choroideus medius (see p. 87) which sends branches, the plexus choroidei laterales, into the lateral ventricles of the secondary fore-brain. The hinder part of the roof bulges upwards and forwards, forming a pouch, the epiphysial pouch, of which the glandula pinealis is the sole remnant in most vertebrates. In many animals, however (certain saurians and selachians), it develops into an organ closely resembling the eye in structure (the parietal eye) which lies underneath the membrane of the skull and is connected by means of a tract of nerve-fibres with the epiphysis.

The corpora mammillaria are externally distinct only in Man and the higher apes. In all other mammals they take the form of a single body, white and globular. The ganglia habenulæ, insignificant in Man, attain a very large size in many mammals.

In no animal is the pulvinar thalami as highly developed as in Man, while, on the other hand, the middle commissure is much more strongly marked throughout the whole series of mammalia.

## 5. THE GREAT BRAIN.

The total (secondary) fore-brain is split by the great longitudinal fissure (see fig. 6) into two equal halves, the hemispheres.

The surface of the hemispheres is almost everywhere covered with grey matter, the cortex. It is depressed into fissures and raised into convolutions, but certain grey masses found in the interior of the great brain will be referred to first.

If the method recommended for exhibiting the optic thalamus has been followed, a rounded swelling freely projecting into the ventricle, the **caudate nucleus** (corpus striatum, intra-ventricular portion of the corpus striatum), *Nc* (fig. 18), is seen to its outer side and separated from it by the stria cornea. It is largest in front of the thalamus, and thins away behind into a narrow riband. This riband, or tail of the nucleus, lies parallel to the stria cornea. It curves backwards, downwards, and, finally, forwards, and can be followed as far as the tip of the temporo-sphenoidal lobe (fig. 17). It thus comes about that the nucleus caudatus describes an arch, the anterior limb of which is formed by the massive head, the pos-



terior limb by the tail. The latter part of the caudate nucleus lies in that portion of the ventricle called the descending horn. If a horizontal section is made through the hemisphere parallel to the surface of the optic thalamus and nucleus caudatus, and only cutting off their domes, a rounded body, about half a centimeter in transverse diameter and projecting (as a rule) backwards into a point, is seen in the anterior part of the thalamus. It is the anterior nucleus (upper nucleus, centre antérieur), *Na*. The fairly distinct capsule which invests the anterior nucleus is prolonged backwards as a plate of white substance, lamina medullaris medialis thalami optici, *Lmm*. This lamina, therefore, divides the thalamus into two pieces of almost equal breadth. The lateral nucleus, *Nl*, projects beyond the

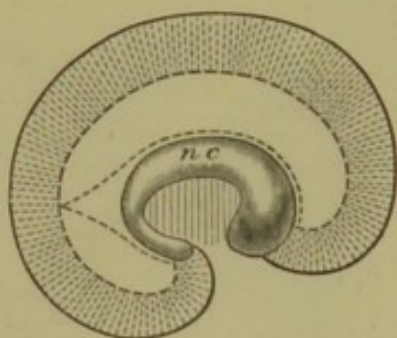


Fig. 17a.—Diagram to show the cortical relations of the nucleus caudatus, *nc* (after Wernicke). The head of the caudate nucleus is in continuity with the cortex of the frontal lobe, the extremity of the tail with that of the temporal lobe.

mesial nucleus (nucleus internus), *Nm*, both in front and behind. The lateral boundary of the thalamus is marked by a white lamella, lamina medullaris lateralis thalami, *Lml*.

If a second horizontal section is made through the hemisphere about  $\frac{1}{2}$  cm. below the surface of the head of the nucleus caudatus (fig. 19), an idea is obtained of the depth to which this grey mass reaches. The nucleus anterior of the thalamus is no longer visible, but the lamina medullaris medialis, *Lmm*, and the nucleus lateralis, *Nl*, are clearly distinguished. The lateral boundary of the thalamus is formed by the feebly-developed lamina lateralis, *Lml*.

Another grey mass appears in this section which nowhere reaches to the surface, but is embedded in white matter, the **lenticular nucleus** (nucleus lenticularis, extra-ventricular portion of the corpus striatum), *Nlf*. It lies like a blunt wedge with its angular border thrust in between the nucleus caudatus and optic thalamus, separated from each of these by the white substance of the internal capsule, *Ci*. Two thin white laminae traverse the nucleus lenticularis, dividing its substance into three segments, which may be named, proceeding from the inner angle outwards, the first, second, and third pieces of the nucleus lenticularis, *Nlf*<sub>1</sub>, *Nlf*<sub>2</sub>, *Nlf*<sub>3</sub>. The mesial and second segments (which together constitute the globus pallidus) of the lenticular nucleus are pale, like the thalamus, while the outer segment or putamen is as dark as the nucleus caudatus. The mesial or first piece is subdivided in most brains into two more or less distinct parts.



The lateral surface of the nucleus lenticularis corresponds in situation to the portion of the cortex of the great brain called the island of Reil, *I*. The nucleus and the cortex are separated by one grey and two white layers. Next to the nucleus lenticularis comes a thin layer of white matter, the outer capsule (capsula externa), *Ce*, to the outer side of which is applied the grey sheet of the claustrum (nucleus tæniæformis), *Cl*.

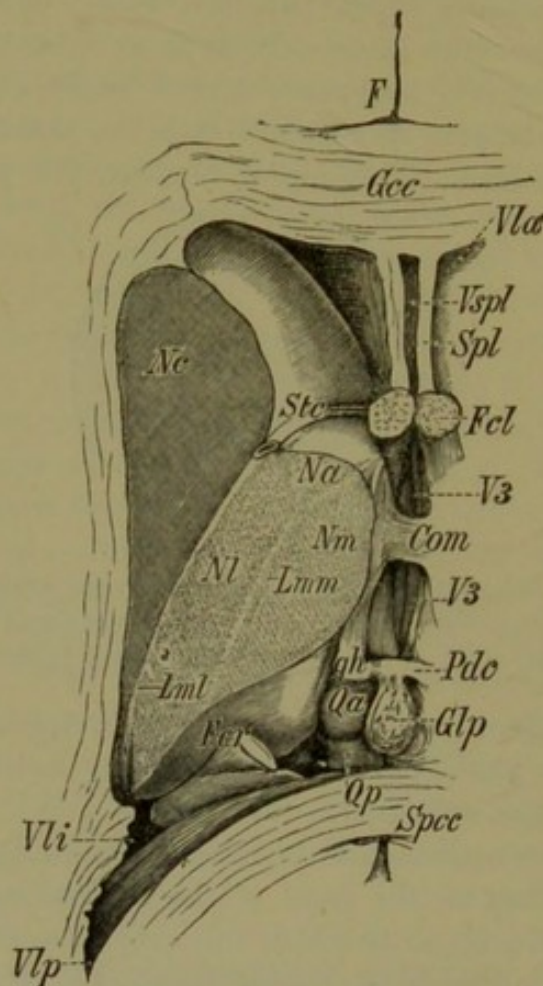


Fig. 18.—Section through the 'tween-brain and the neighbouring part of the fore-brain half a centimeter beneath the upper surface of the optic thalamus and nucleus caudatus (*nat. size*). Only the thalamus, the nucleus caudatus, and the parts immediately surrounding them are represented.—*Com*, Commissura mollis; *Fcl*, columna fornicis; *Fer*, crus fornicis; *Gcc*, genu corporis callosi; *gh*, ganglion habenulæ; *Glp*, glandula pinealis; *Lml*, lamina medullaris lateralis; *Lmm*, lamina medullaris medialis; *Na*, nucleus anterior; *Nc*, nucleus caudatus; *Nl*, nucleus lateralis; *Nm*, nucleus medialis; *Pdc*, pedunculus pinealis; *Qa*, anterior corpus quadrigeminum; *Qp*, posterior corpus quadrigeminum; *Spcc*, splenium corporis callosi; *Spl*, septum pellucidum; *Stc*, stria cornea; *Vla*, anterior horn of lateral ventricle; *Vli*, descending horn of lateral ventricle; *Vlp*, posterior horn of lateral ventricle; *Vspl*, ventriculus septi pellucidi; *V3*, third ventricle.

Between the claustrum and the cortex of the island of Reil lies the sheet of white matter termed lamina fossæ Sylvii (capsula extrema). The mesial surface of the claustrum corresponds to the outer surface of the nucleus lenticularis, its lateral surface adapts itself to a certain extent to the cortex of the island of Reil, exhibiting similar small elevations and depressions.







*Wernicke*; *frv*, frenulum veli anterioris; *G*, genu capsulae internae; *Gcc*, genu corporis callosi; *H*, gyrus hippocampi; *I*, island of Reil; *Lml*, lamina medullaris thalami lateralis; *Lmm*, lamina medullaris thalami medialis; *M*, great longitudinal fissure; *Nc*, nucleus caudatus (head); *Nc'*, nucleus caudatus (tail); *Nl*, nucleus lateralis thalami; *Nlf*, nucleus lenticularis; *Nlf 1* and *2*, globus pallidus; *Nlf 3*, putamen; *Nm*, nucleus medialis thalami; *Ntg*, nucleus tegmenti ruber; *O*, occipital lobe; *P*, parietal lobe; *Pu*, pulvinar; *Qa*, anterior corpus quadrigeminum; *Qp*, posterior corpus quadrigeminum; *Spl*, septum pellucidum; *Ss*, sagittal fibres of occipital lobe; *Tp*, tapetum; *Tt*, gyrus temporalis transversus; *VA*, Vicq d'Azyr's bundle; *Vla*, anterior horn of lateral ventricle; *Vli*, inferior horn of lateral ventricle; *Vspl*, ventriculus septi pellucidi; *V3*, ventriculus tertius.

The anterior angle of the nucleus lenticularis is situate somewhat farther back than the front of the nucleus caudatus. The posterior angle lies a little behind the thalamus. In sections taken on other planes its sagittal diameter is less.

To get a complete picture of the nucleus lenticularis, a frontal (transverse vertical) section must be made through the hemisphere at the level of the front of the thalamus (fig. 20). It now appears as a wedge, with its convex base resting on the cortex of the island of Reil; its angle—more acute than in a horizontal section—is directed beneath the thalamus. Between the nucleus and the cortex is again seen the claustrum shut in between the external capsule and the lamina fossae Sylvii.

The region which lies below the thalamus (regio subthalamica), seen in this section, and sections carried more posteriorly, contains both grey and white matter; and can only be treated of when we are dealing with the minute structure of the brain. If a section is carried a little farther forward than in fig. 20, so that it traverses the optic chiasm, the lateral segment of the nucleus lenticularis is seen, better than in this section, to be in direct relation to another grey mass, the nucleus amygdaleus (nucleus amygdaliformis), *Am*. This nucleus is understood to be a thickened portion of the cortex of the temporo-sphenoidal lobe. [The claustrum also is fused at its anterior end with the nucleus amygdaleus.]

The tractus opticus, *II*, in its course around the cerebral peduncle pushes itself in between the nucleus lenticularis and nucleus amygdaleus.

The **white matter of the hemisphere** reaches its greatest development above the central ganglia (or basal ganglia, a term comprehending nuclei caudatus et lenticularis and the optic thalamus). In a horizontal section parallel to, but above, the upper surface of the corpus callosum, the whole central mass of the hemisphere appears white (centrum semiovale Vieussenii). Such a section is not figured, but a frontal section of the centrum is seen in fig. 20, *CsV*. In deeper sections, which pass through the included grey masses (fig. 19), the white matter is seen to be broken up into limited tracts, which invest the lenticular nucleus, as the internal and external capsules. The former is seen in a horizontal section to consist of two segments meeting one another at an oblique angle, the knee (genu) of the internal capsule, *G*. The two segments are distinguished as



the anterior limb, *Cia*, compressed between the nucleus lenticularis and the nucleus caudatus, and the posterior limb, *Cip*, between the nucleus lenticularis and the optic thalamus.

Certain special masses of white matter—the corpus callosum, fornix, and anterior commissure—must now be described.

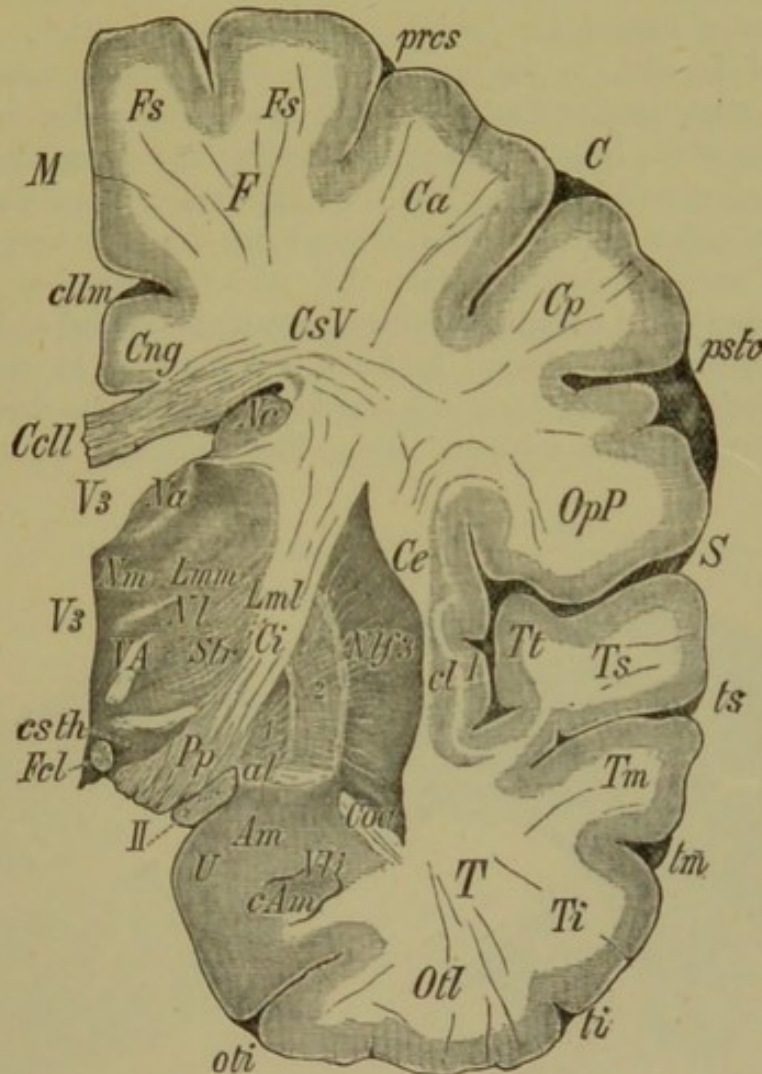


Fig. 20.—Frontal section through the human cerebral hemisphere. Left side, posterior portion (*natural size*).—II, Tractus opticus; *al*, situation of ansa lenticularis; *Am*, amygdala; *C*, central fissure; *Ca*, gyrus centralis anterior; *cAm*, anterior end of cornu Ammonis; *Ccl*, corpus callosum; *Ce*, capsula externa; *Ci*, capsula interna; *cl*, claustrum; *clm*, sulcus calloso-marginalis; *Cng*, gyrus fornicatus; *Coa*, commissura anterior; *Cp*, gyrus centralis posterior; *csth*, corpus subthalamicum; *CsV*, centrum semiovale Vieussensii; *F*, frontal lobe; *Fcl*, anterior pillar of fornix; *Fs*, gyrus frontalis superior; *I*, island of Reil; *Lmm*, *Lml*, lamina medullaris medialis et lateralis; *M*, great horizontal fissure; *Na*, *Nm*, *Nl*, nucleus anterior, medialis et lateralis thalami optici; *Nc*, nucleus caudatus (tail); *Nlf* 3, 2, 1, the three portions of the nucleus lenticularis; *OpP*, opercular portion of inferior parietal lobule; *oti*, sulcus occipito-temporalis inf.; *Otl*, gyrus occipito-temporalis lateralis; *Pp*, pes pedunculi; *prcs*, sulcus præcentralis, pars superior; *pslc*, sulcus postcentralis; *S*, fissura Sylvii; *Str*, stratum reticulare; *T*, temporal lobe; *Tt*, gyrus temporalis transversus; *Ts*, *Tm*, *Ti*, gyrus temporalis superior, medius et inferior; *ts*, *tm*, *ti*, sulcus temporalis superior, medius et inferior; *U*, uncus gyri hippocampi; *VA*, bundle of Vicq d'Azyr; *Vli*, anterior end of the inferior horn of the lateral ventricle; *V3*, ventriculus tertius.



(a.) **The Corpus Callosum.**—If the two hemispheres are pressed apart, a white structure of from 7 to 9 cm. in sagittal diameter is seen crossing the bottom of the longitudinal fissure.

Its fibres exhibit a transverse arrangement, *Cell*. In addition to the transverse fibering, two thin bundles of longitudinal fibres lie on its upper surface, striæ longitudinales mediales (nervi Lancisii), *NL* (fig. 23), and between them a furrow, the raphe (sutura corporis callosi). Laterally to the nerve of Lancisi, in the angle below the gyrus fornicatus, another thickening, stria longitudinalis lateralis seu tænia tecta, is often seen stretching the whole length of the corpus callosum. From that portion of the corpus callosum seen at the bottom of the fissure, its substance radiates outwards on either side into the hemispheres (radiatio corporis callosi). Above the corpora quadrigemina, the posterior edge of the corpus callosum is, as seen in a sagittal section, roundly thickened and rolled over, splenium corporis callosi, *Spec*. In front it turns over in the knee (genu corporis callosi), *Gcc*, and becoming quickly thinner folds downwards and backwards to form the rostrum, *Rcc*. The radiation outwards of the

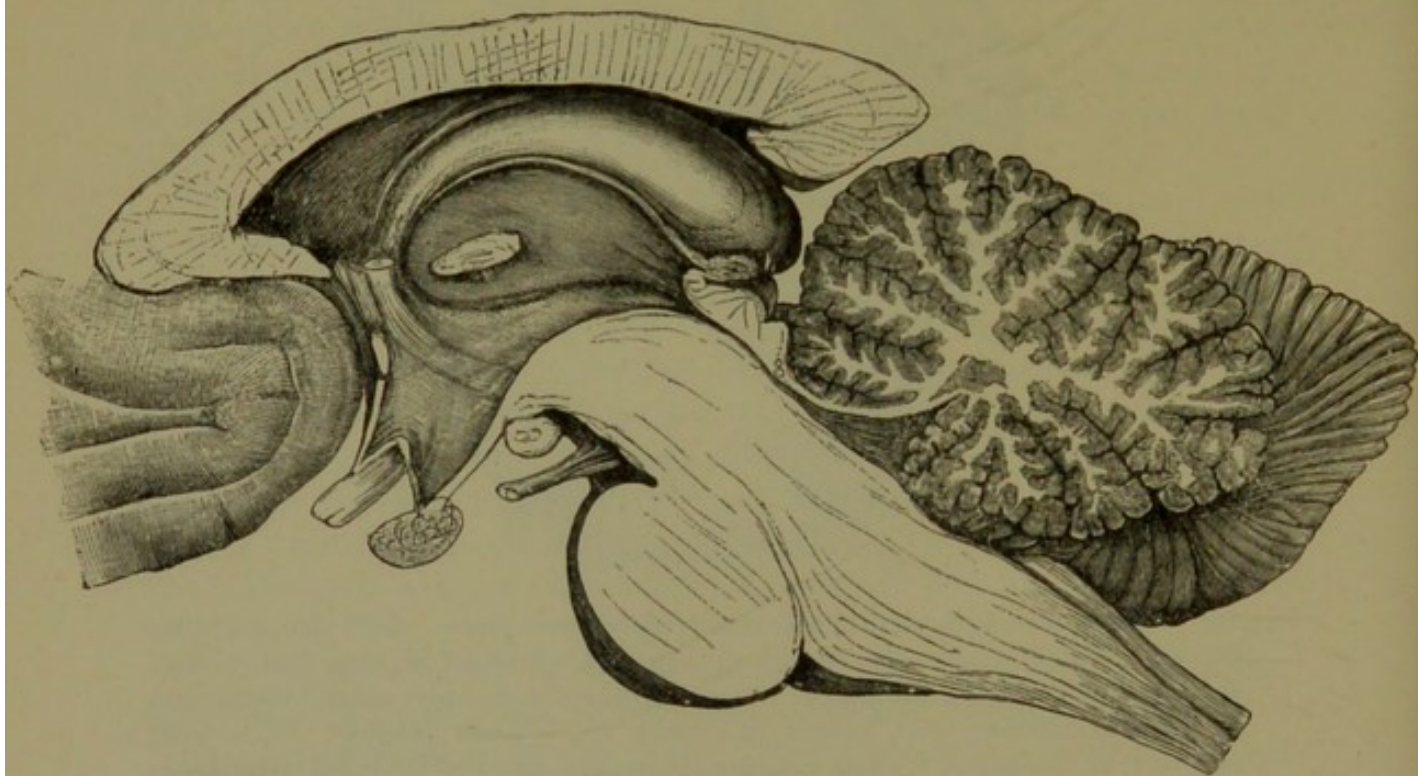
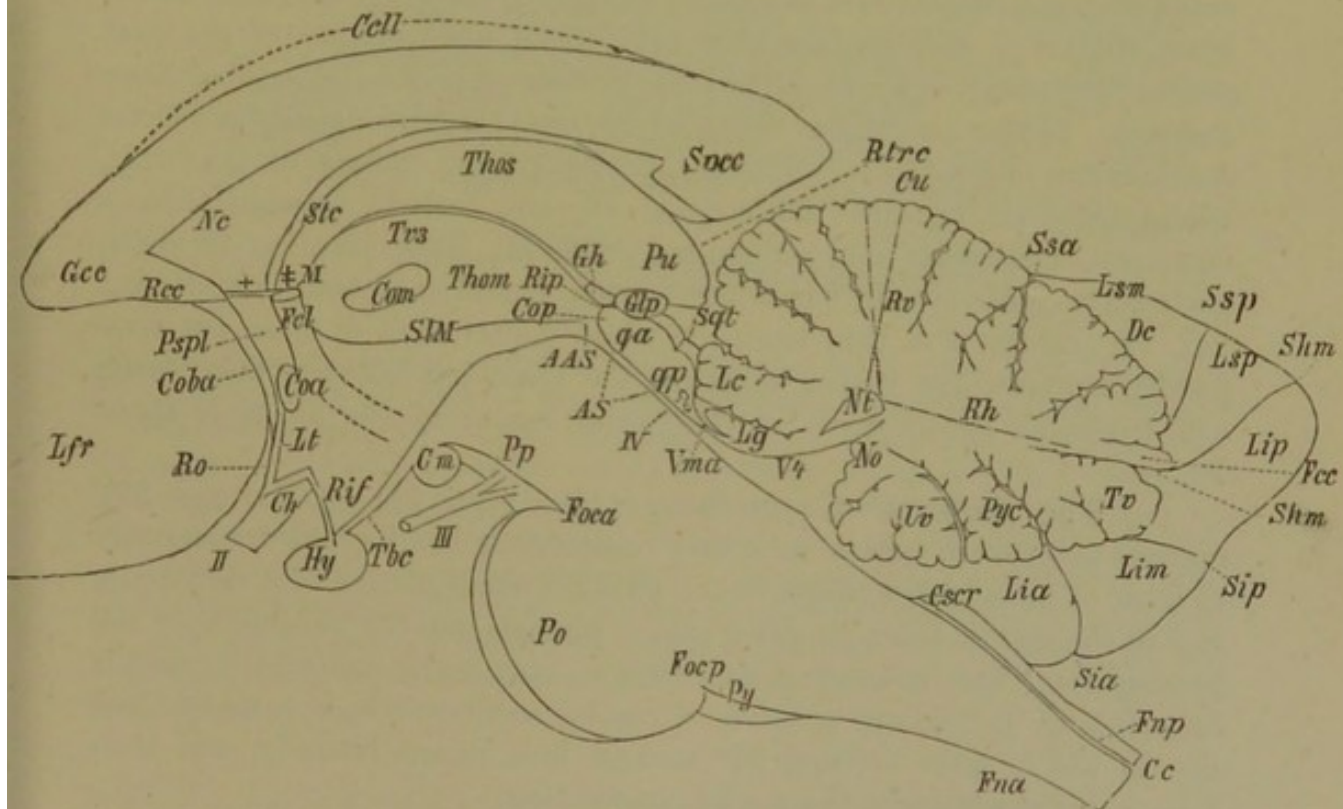


Fig. 21.—Sagittal section through the brain in the median line, right half (*natural size*). Of the convolutions on the mesial surface of the hemisphere, only a part of those in the frontal region are visible (*Lfr*).—*II*, Nervus opticus; *III*, nervus oculomotorius; *IV*, crossing of the n. trochlearis; *AAS*, aditus ad aquæductum Sylvii; *AS*, aquæductus Sylvii; *Cc*, canalis centralis; *Cell*, corpus callosum; *Ch*, chiasma nervorum optidorum; *Cm*, corpus mammillare; *Coa*, commissura ant.; *Coba*, commissura baseos alba; *Com*, commissura mollis; *Cop*, commissura posterior; *Cscr*, calamus scriptorius; *Cu*, culmen; *De*, declive; *Fcc*, folium cacuminis; *Fcl*, columna fornicis cut across at  $\pm$ ; *Fna*, funiculus ant. med. spinalis; *Fnp*, funiculus post. med. spin.; *Foca*, foramen cæcum ant.; *Focp*, foramen cæcum post.; *Gcc*, genu; *Gh*, ganglion habenulæ; *Glp*, glandula pinealis; *Hy*, hypophysis; *Lc*, lobulus centralis; *Lg*, lingula; *Lia*, lobus inf. ant.; *Lim*, lobus inf. med.; *Lip*, lobus inf. post.; *Lsm*, lobus sup. med.; *Lsp*, lobus sup. post.; *Lt*, lamina ter-



corpus callosum will be described later on. Between the rostrum and genu of the corpus callosum in front, and the fornix behind, is shut in a thin triangular plate of nerve-substance, septum pellucidum, *Splc*. This plate consists of two layers which contain between them a median cleft, the fifth ventricle (ventriculus septi pellucidi), *Vspl* (figs. 18 and 19). The size of this ventricle varies to a not inconsiderable extent in different individuals. The lower angle of the septum is continued between the rostrum and the fornix, as the pedunculus septi pellucidi, *Pspl* (figs. 21 and 23), and reaches the base of the brain at the mesial corner of the substantia perforata anterior, which it crosses on its way to the tip of the temporal lobe. In fig. 21 the septum pellucidum and fornix are marked with the signs + and  $\pm$ . The principal part of both has been removed in this preparation.

(b.) **Fornix** (voute à trois ou quatre piliers, trigone cérébral) appears as a paired structure composed of longitudinal fibres, which lies on the under surface of the corpus callosum, and arches over the thalamus (fig. 22). The fornix comes up out of the descending horn of the lateral



minalis; *M*, situation of foramen of Monro; *Nc*, nucleus caudatus; *No*, nodulus; *Nt*, nucleus tecti; *Po*, pons; *Pp*, pes pedunculi; *Pspl*, pedunculus septi pellucidus; *cut* at +; *Pu*, pulvinar thalami; *Pyc*, pyramis cerebelli; *qa*, corpus quadrigeminum anterius; *qp*, corpus quadrigeminum posterius; *Rcc*, rostrum; *Rh*, ramus medullaris horizontalis; *Rif*, infundibulum; *Rip*, recessus infra-pinealis; *Ro*, recessus opticus; *Rtrc*, rima transversa cerebri; *Rv*, ramus medullaris verticalis; *Shm*, sulcus horizontalis magnus; *Sia*, sulcus inf. ant.; *Sip*, sulcus inf. post.; *SlM*, sulcus Monroi; *Spcc*, splenium; *Sqt*, sulcus corp. quad. transversus; *Ssa*, sulc. sup. ant.; *Ssp*, sulcus sup. post.; *Stc*, stria cornea; *Tbc*, tuber cinereum; *Thom*, thalamus opticus, mesial surface; *Thos*, thalamus opticus, upper surface; *Tv*, tuber valvulae; *Tv3*, tænia ventriculi tertii; *Uv*, uvula; *Vma*, velum medullare ant.; *V4*, fourth ventricle.



ventricle as a flat band attached to the brain-wall by one of its edges only. In this situation it is termed the fimbria, *Fi*. Converging towards its fellow of the opposite side it reaches the under surface of the corpus callosum a little in front of the splenium. The free portions constitute the crura fornicis (posterior pillars of the fornix), *Fcr*. The two pillars are separated from the thalamus by the interval of the third ventricle.

The two crura of the fornix unite a little in front of the posterior commissure. From this spot forwards they constitute a single band, the body of the fornix, *Fcp*, about 20 to 25 mm. long, firmly united to the corpus callosum. In front the septum pellucidum is pushed in between the fornix and the corpus callosum. Anteriorly, the fornix splits into two rounded columns (columnæ fornicis, anterior pillars), *Fcl* (figs. 18, 19, 20, and 21), which pass backwards as well as downwards, being covered with a thin layer of grey substance belonging to the thalamus. If this grey investment is removed the columns of the fornix can be followed as well-defined white tracts as far as the corpora mammillaria (radix ascendens fornicis), fig. 21. Another bundle (bundle of Vicq d'Azyr, figs. 19 and 20, *VA*) fasciculus thalamo-mammillaris, ascending from each corpus mammillare to the optic thalamus, can be laid bare by a little manipulation of the grey matter. Making a slight lateral inclination it reaches the tuberculum anterius. Earlier anatomists regarded this fibre-tract erroneously as a direct continuation of the fornix. The two posterior crura (pillars) of the fornix, where they lie beneath the corpus callosum, include between them a structure, triangular and equilateral, with an angle pointing forwards, psalterium (lyra Davidis, fornix transversus, commissura Ammonis), *Ps* (fig. 24). It consists of a thin lamina of white matter, and is often not completely united to the corpus callosum, the space left between them being called *Verga's* ventricle, *VV*. The total length of the fornix is about 10 cm.

(c.) **The Anterior Commissure**, *Coa* (figs. 12, 19, 21, and 22), appears in median section as a very conspicuous bundle, cut transversely in front of the anterior pillars of the fornix, a small portion of it only being free in the middle line; on either side it plunges into the substance of the hemisphere. The anterior commissure is very easily followed by simple dissection or by making a series of frontal sections. It is a well-defined bundle which, after crossing the median line, passes laterally, and then arches backwards under the nucleus lenticularis.

[In a hardened brain, owing to the shrinking of its fibres, the anterior commissure lies almost free in the channel which it occupies in its course through the great brain. With any blunt instrument it can be followed beneath the neck of the nucleus caudatus, across the internal capsule and through the nucleus lenticularis, which it pierces at the back of its middle segment, missing the internal, but traversing the external segment. It exhibits a remarkable torsion, its fibres being twisted upon one another in such a manner as to suggest that while the middle portion was fixed the two ends of the bundle have been rotated upwards and backwards (see Appendix A, Rotation of Great Brain). This commissure makes



its appearance at an early stage in the development of the brain. It appears to be present in all vertebrates, attaining a greater relative importance amongst the lower members of the sub-kingdom, in which the cortex of the great brain and its special commissure, the corpus callosum, are rudimentary, than in Man.]

The part of the **base of the fore-brain**, which lies in front of the optic chiasm, must now be treated of in further detail (fig. 23). The lateral and mesial portions of this surface will be separately described. On either side lies a light grey area, bounded behind by the optic tract, in front by the frontal convolutions, and laterally by the temporo-sphenoidal

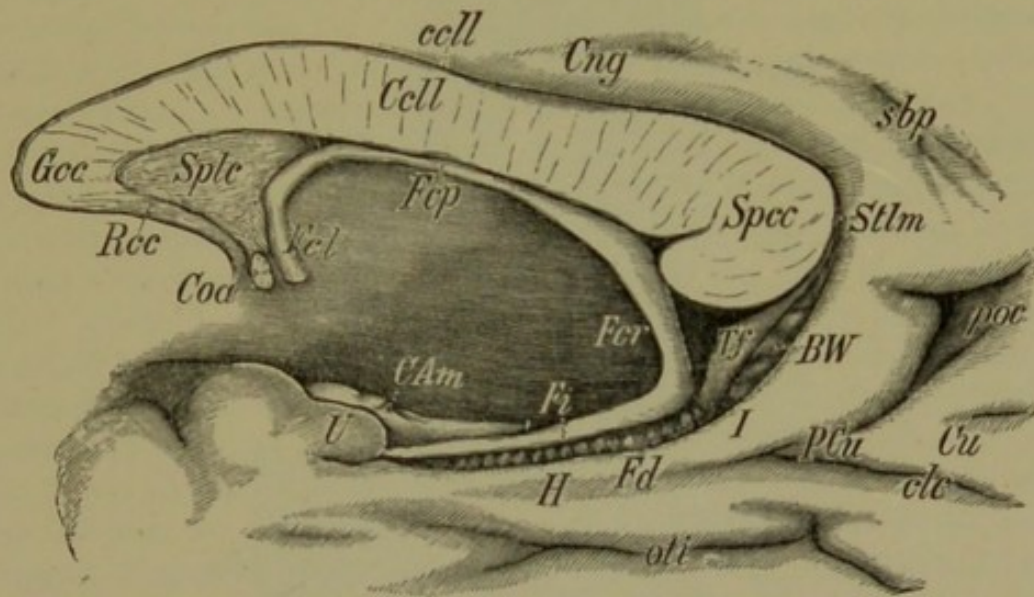


Fig. 22.—Part of a median section through the great brain. The optic thalamus is broken away; the parts of the temporal lobe are somewhat separated from one another (*natural size*).—*BW*, Gyrus subcallosus; *CAm*, cornu Ammonis; *Cell*, corpus callosum; *ccll*, sulcus corporis callosi; *clc*, fissura calcarina; *Cng*, gyrus cinguli; *Coa*, commissura anterior; *Cu*, cuneus; *Fcl*, columna fornicis; *Fcp*, corpus fornicis; *Fer*, crus fornicis; *Fd*, fascia dentata; *Fi*, fimbria; *Gcc*, genu corporis callosi; *H*, gyrus hippocampi; *I*, isthmus gyri fornicati; *oti*, sulcus occipito-temporalis inferior; *PCu*, pedunculus cunei; *poc*, fissura parieto-occipitalis; *Rcc*, rostrum corporis callosi; *sbp*, sulcus subparietalis; *Spcc*, splenium corporis callosi; *Sple*, septum pellucidum; *Stlm*, stria longitudinalis medialis; *Tf*, tuberculum fasciæ dentatæ.

lobe, *T*; this is known as the substantia perforata anterior (lamina cribrosa), fig. 23, *Spa*. Numerous apertures for vessels are seen in this region, especially in its antero-lateral portion. It is these holes which have given the area its name. Separate white bundles, emerging from the side of the temporo-sphenoidal lobe, cross this area, as well as the transverse orbital convolution, to reach the free white column of the olfactory tract, *Trol*. The olfactory tract passes forwards and slightly inwards for a distance of about 3.5 cm. At its anterior end it bears a yellowish-grey swelling, the olfactory bulb (bulbus nervi olfactorii), *Bol*. The median portion of this part of the base of the brain, in front of the optic chiasm, is narrower than the substantia perforata, but reaches farther forwards; it constitutes the



most anterior portion of the floor of the third ventricle (or grey floor-commissure).

The part which lies immediately in front of the chiasm is very easily torn; it is named the lamina terminalis, *Lt*, fig. 23 (see also fig. 21). A slight transverse elevation is produced by the anterior commissure, here covered by a thin layer of grey matter.

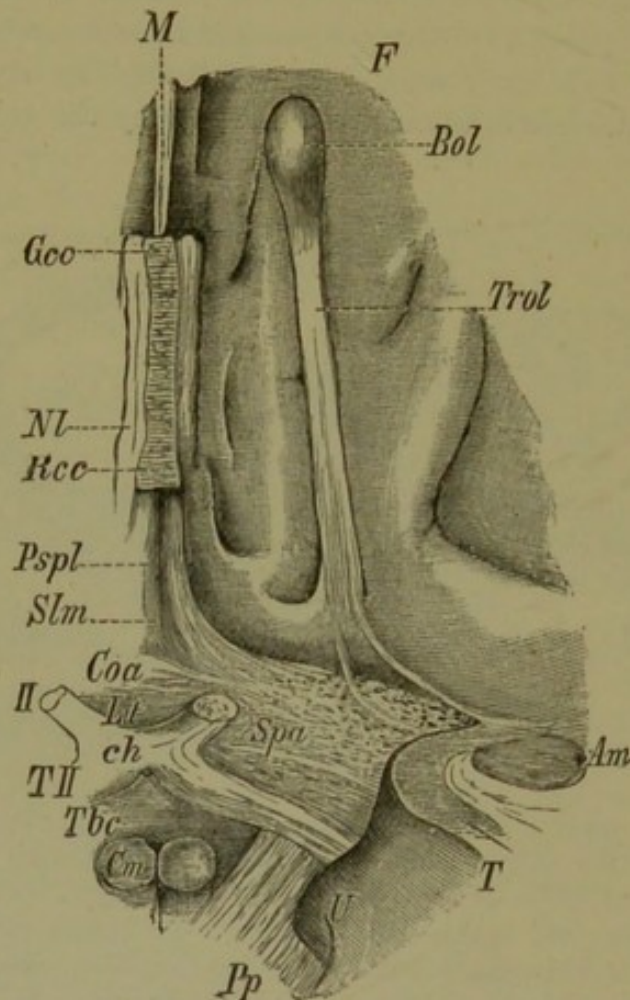


Fig. 23.—Part of the base of the brain, the left hemisphere in front of the optic chiasm. The apex of the temporal lobe is cut away.—II, Nervus opticus; *Am*, nucleus amygdaleus; *Bol*, bulbus olfactorius; *ch*, chiasma; *Cm*, corpus mamillare; *Coa*, elevation in the grey commissure of the floor of the third ventricle caused by the underlying anterior commissure; *F*, frontal lobe; *Gcc*, genu corp. callosi; *Lt*, lamina terminalis; *M*, longitudinal fissure; *NL*, nervus Lancisii; *Pp*, pes pedunculi; *Pspl*, pedunculus septi pellucidi; *Rcc*, rostrum corporis callosi; *Slm*, sulcus medius subst. perf. ant.; *Spa*, substantia perforata anterior; *T*, temporal lobe; *Tbc*, tuber cinereum; *Trol*, tractus olfactorius; *TII*, tractus opticus; *U*, uncus.

In front of this grey elevation is seen a furrow, sulcus medius substantiæ perforatæ anterioris, *Slm*, which extends to the rostrum corporis callosi, *Rcc*. On either side of the median furrow is seen a thin longitudinal swelling which emerges from under the rostrum, gradually broadens and follows the direction of the brain-cortex backwards; pedunculus septi pellucidi, *Pspl*. Its hinder end turns outwards, crossing the perforated space towards the tip of the temporal lobe. In most cases its course is difficult to follow.



The first rudiments of the primary and secondary fore-brain have been already described. The next stage is the formation of a great thickening (nucleus caudatus and nucleus lenticularis) in the floor of the primary fore-brain. This mass of grey matter, single at first, is presently divided into two parts by a broad fibre-tract which starts from the brain-cortex and passes through the midst of it on its way to the spinal cord. The upper mesial part, projecting freely into the ventricle, becomes the nucleus caudatus, the lateral and lower part forms the nucleus lenticularis. The fibre-tract itself supplies the inner capsule. In treating of the development of the 'tween-brain (p. 74) we were forced, moreover, to anticipate our later observations by speaking of the tela choroidea media. Where the roof of the 'tween-brain (and of the primary fore-brain also), which remains thin in every stage of development, borders on the later developed secondary anterior vesicle, a thickened arch of nerve-fibres appears—the fornix. The corpus callosum comes into existence comparatively late, and in the following fashion:—The mesial surfaces of the two anterior vesicles, which face each other, unite half-way up only, the upper and lower portions of each of them remaining detached. (This, at least, is the case in the anterior part.) At the junction of the two, certain fibres (the fibres of the corpus callosum) pass from one hemisphere to the other. The cleft between the two vesicles is thus broken up into an open space above, the longitudinal fissure, and a closed space below, the ventriculus septi pellucidi. The septum pellucidum, or that part of the wall of the cerebral vesicle which is cut off from the free general surface by the development of the corpus callosum, remains rudimentary in structure. The secondary anterior cerebral vesicles, which attain a remarkably high development in Man, form, as has been shown, the brain-mantle or pallium. They are completely invested with grey matter—the cortex. From the under surface of each hemisphere a hollow off-shoot grows out, directed forwards, its interior cavity communicating with the anterior horn of the lateral ventricle. This is the lobus olfactorius. In Man the cavity or ventriculus lobi olfactorii fills up at a later period, but indications of it still remain.

We owe to *Edinger* our knowledge of the behaviour of the several parts of the brain throughout the vertebrata. He has shown that a secondary fore-brain does not develop from the primary anterior vesicle in all. In the rays the frontal wall of the primary fore-brain merely thickens, often growing into a very large and massive structure, and including the stem-ganglion. In many sharks we can recognise in the small paired out-growths in front of this mass the first rudiments of the hemispheres. In osseous fishes we find an immense stem-ganglion, the corpus striatum, at the base of the fore-brain (at one time erroneously held to be the actual hemispheres of the cerebrum), while the dorsal portion of the anterior vesicle, the pallium, is represented only by a thin layer of epithelium, which is destroyed by the ordinary methods of preparation.

Proceeding upwards in the scale, we find in all vertebrates a clearly-defined brain-mantle arching over the basal stem; and the higher we ascend



the more highly developed are both the grey cortex and the white substance it encloses.

In most animals the lobi olfactorii are far more highly developed than in Man. In cartilaginous fishes, especially, we meet with bulbi olfactorii of enormous size. Birds have, on the whole, but little sense of smell, and the development of the region which subserves this sense is correspondingly slight. I shall discuss the central olfactory organs of mammals in detail when I come to describe the first pair of cerebral nerves.

In lower mammals the corpus callosum is poorly developed. In Monotremes and Edentates it is hardly distinguishable, and in Submammalia it is altogether absent. [There is no corpus callosum in non-placental mammals.]

The fornix looks comparatively large in many mammals, the more so from the fact that the grey substance of the cornu Ammonis extends far to the front, along the fornix and above the thalamus.

## 6. THE VENTRICLES OF THE GREAT BRAIN.

Although the anatomical disposition of the ventricles of the great brain seems simple, their morphological relations to the nervous substance are only to be made out by careful ontogenetic study.

The ventricles of the brain can be entered from behind beneath the splenium corporis callosi. However much the transverse slit which here exists ([*incisura marsupii*] *fissura transversa cerebri anterior*, *rima transversa*, *fissura Bichati*) is closed up by the membranes of the brain, it yet affords this opening. The first thing which meets the view when one removes the back of the brain, with the corpus callosum and body of the fornix (on one side at any rate the fornix should be left for further study), is not the optic thalamus but a vascular membranous fold which covers it. Seen in its whole extent at once this fold has the form of an equilateral triangle. The base of the triangle corresponds with the transverse fissure; its apex reaches the anterior pillars of the fornix; its antero-lateral borders lie parallel to the *striæ corneæ* and somewhat mesial to them, and are attached to the surface of the thalamus (fig. 24); this fold of membrane is the *tela choroidea superior* (*velum triangulare* [*seu interpositum*]), *Tcs*. The lateral margin of the *tela choroidea* carries a convoluted system of blood-vessels, more extensive behind than in front, the choroid plexus of the great brain, *Plchl*. At the junction of the lateral and posterior borders of the *tela choroidea* the plexus attains its greatest development, swelling into the so-called *glomus*. From this angle of the *tela* the choroid plexus is continued downwards, and finally forwards [around the cerebral peduncle], following the course of the *crus fornicis* as far as the anterior point of that portion of the lateral ventricle, which we shall learn presently to call the descending horn.

If the fornix, *F*, has not been removed, one notices that its sharp lateral border is attached to the *tela choroidea* along a line parallel to, but slightly



on the mesial side of, the stria cornea and the line of attachment of the tela to the thalamus. Where it lies by the side of the plexus choroideus the tela choroidea shrinks into a thin lamella of white matter (*lamina affixa*, *Laf*), firmly attached to the surface of the thalamus. It can be followed as far as the mesial side of the stria cornea.

On the under side of the tela choroidea, near the middle line, are attached two narrow strips of choroidal plexus, plexus choroidei medii,

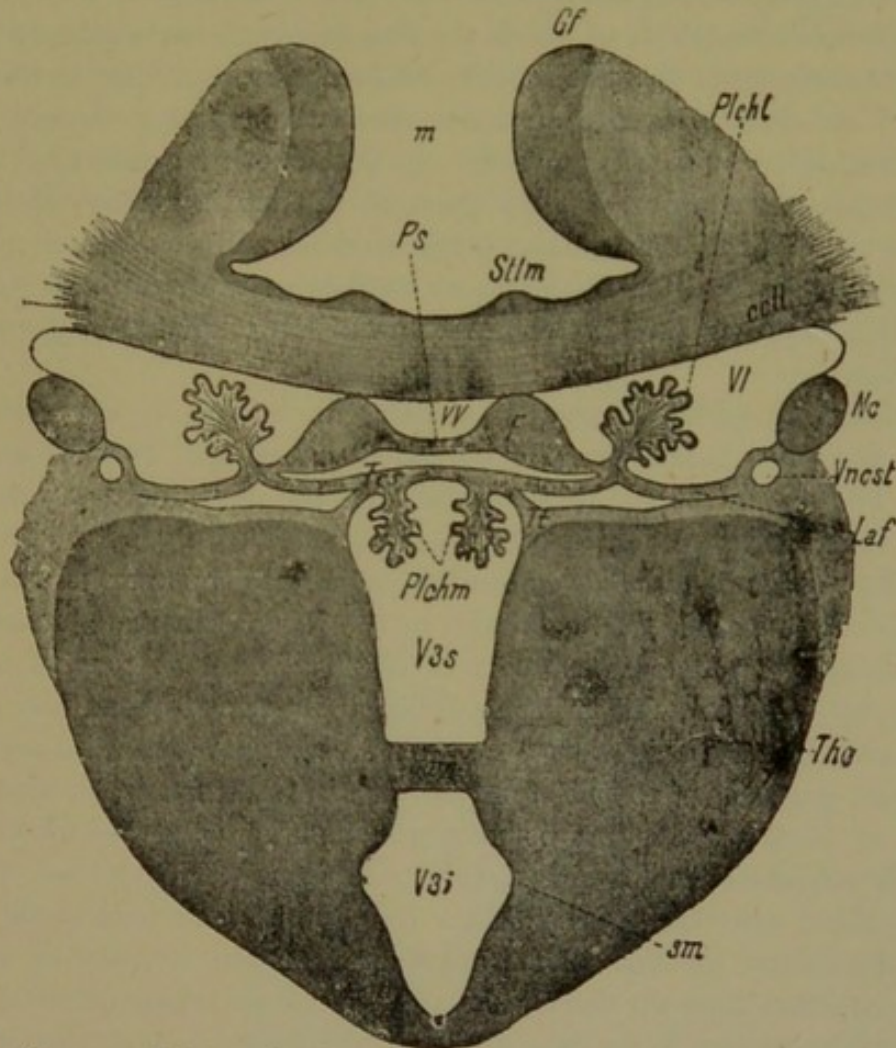


Fig. 24.—Diagram of the cerebral ventricles and the plexus choroideus medius.—*cell*, Corpus callosum; *com*, commissura mollis; *F*, fornix; *Gf*, gyrus fornicatus; *Laf*, lamina affixa (its union with the thalamus extends farther than is shown in the drawing, to the plexus choroideus); *m*, great longitudinal fissure; *Nc*, nucleus caudatus; *Plchl*, plexus choroideus lateralis; *Plchm*, plexus choroideus medialis; *Ps*, psalterium; *sm*, sulcus Monroi; *Tcs*, tela choroidea superior; *Tho*, thalamus opticus; *Tt*, tænia thalami; *Vl*, ventriculus lateralis; *V3s* and *V3i*, third ventricle (*s* and *i*, its superior and inferior portion respectively); *Vncst*, vena striæ corneæ; *VV*, Verga's ventricle.

*Plchm*. They extend from the anterior angle of the tela to its base. Attached to the sharp ridge formed by the junction of the vertical and horizontal surfaces of the thalamus opticus is a thin platelet of white matter, tænia thalami, *Tt*. It passes over into the plexus choroideus medius.

The whole hollow space in the interior of the great brain is divided into



three portions by the attachments of the tela to the thalami, a middle, *V3*, and two symmetrical lateral ventricles, *Vl*.

There are, besides, other spaces more or less considerable, to which little or no regard is usually paid. They may, nevertheless, prove of great importance, especially in pathological conditions. In the diagram (fig. 24) their extent is purposely exaggerated. First, in the middle line and between the under surface of the corpus callosum and the psalterium, we find a cleft which is sometimes large enough to deserve the name of a cavity. This cavity is *Verga's* ventricle, of which mention has been made already (p. 81). The under surfaces of the psalterium and fornix are attached to the upper surface of the tela choroidea by loose connective-tissue, and, still in the middle line, below *Verga's* ventricle, we find another space, generally of inconsiderable dimensions. That part of the under surface of the tela choroidea which lies between the tænia thalami and the lamina affixa is attached in similar fashion to the upper surface of the thalamus. A space is thus left at either side, which might well be designated spatium infra-choroideum.

The third or middle ventricle, *ventriculus tertius*, is a vertical cleft between the grey mesial surfaces of the thalamus (fig. 24, *V3s* and *V3i*, and figs. 18, 19, and 20). At its hinder end the aquæductus Sylvii opens into the ventricle at the aditus ad aquæductum, *AAS* (fig. 21). From this spot its floor sinks downwards somewhat quickly to the apex of the infundibulum. The anterior wall is formed by the lamina cinerea terminalis, *Lt*, already described. The lowest part of this surface is so pushed into the ventricle by the optic chiasm, that a pouch is formed above the chiasm, *recessus chiasmatis (seu opticus)*, *Ro*. In front, where the stria medullaris approaches quite close to the anterior pillar of the fornix, a wide space, foramen of *Monro*, *M*, is left between the thalamus and the fornix. The plexus choroideus lateralis with a vein passes out of the lateral ventricle into the third ventricle through this hole, and bends backwards in the plexus choroideus medius. The foramen of *Monro* constitutes the only direct connection between the middle and lateral ventricles (see also fig. 6).

A shallow groove is to be noticed on the mesial face of the thalamus, which passes in a gentle curve beneath the commissura mollis, from the foramen of *Monro* to the aditus ad aquæductum Sylvii, sulcus *Monroi seu hypothalamicus*, *SLM* (fig. 21).

The paired LATERAL VENTRICLES (*ventriculi laterales seu tricornes*), *Vl*, lie in the interior of each hemisphere, and communicate through the foramen of *Monro* with the middle ventricle; they are not directly in connection with one another.

Just as the whole hemisphere in the human brain is to be looked upon as presenting an arch open in front with a posterior prolongation, the occipital lobe, so the cavity which it contains is an arched space with a special occipital prolongation backward.

In each lateral ventricle (figs. 12, 18, and 19) is distinguished a central or principal part (*cella media*), from which a horn (anterior horn, *Vla*) passes forwards, a diverticulum is continued backwards (posterior horn,



*Vlp*), and, lastly, the ventricle ends in the inferior limb of the arch, the inferior [or descending] horn, *Vli*.

The **anterior horn** is the part of the lateral ventricle which corresponds to the head of the nucleus caudatus, and reaches still farther forwards into the frontal lobe. Its mesial wall is formed by the septum pellucidum. The corpus callosum constitutes its front wall and roof.

The **cella media** begins at about the level of the foramen of Monro. Its roof is formed by the middle portion of the body of the corpus callosum. In the floor of the cavity lie, in order from without inwards, the tail of the nucleus caudatus, the stria cornea, the lamina affixa (its apparent connection with the upper surface of the thalamus is deceptive), and the plexus choroideus lateralis (figs. 12 and 24). The upper surface of the fornix may also be included in the floor of the cella media, since this structure lies with only its mesial edge resting against the corpus callosum.

The **posterior horn** of the lateral ventricle (fig. 25) begins at about the level of the splenium corporis callosi, and reaches usually nearly to the

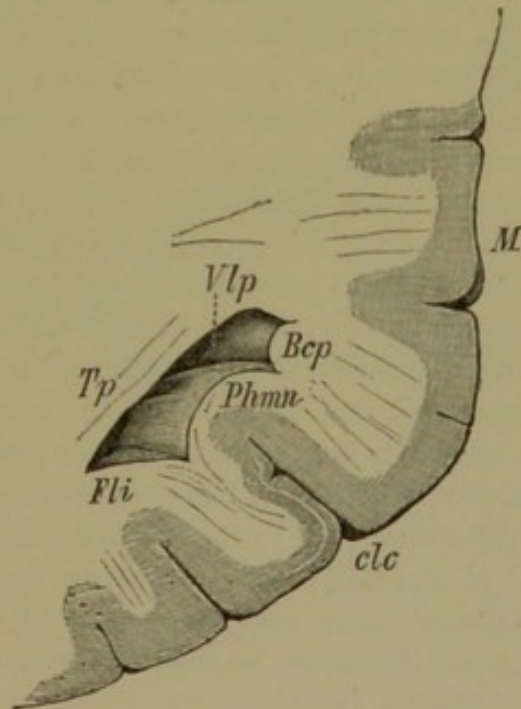


Fig. 25.—Frontal section through the right cerebral hemisphere, behind the splenium corporis callosi. *Posterior segment.* (Natural size.)—*M*, Mesial surface of the hemisphere; *clc*, fissura calcarina; *Vlp*, posterior horn of the lateral ventricle; *Bcp*, bulbus cornu posterioris; *Phmn*, pes hippocampi minor; *Fli*, fasciculus longitudinalis inf.; *Tp*, tapetum.

occipital pole of the hemisphere. For upper and outer walls the posterior horn has the continuation of the corpus callosum or tapetum, *Tp*, below which lies the bulk of the fasciculus longitudinalis inferior. The mesial and lower wall is formed, as shown in a frontal section, by three more or less distinct elongated elevations. The upper corresponds to the margin of the corpus callosum, forceps posterior corporis callosi (bulbus cornu posterioris), *Bcp*. The middle swelling, calcar avis (pes hippocampi minor), *Phmn*, is formed by a fissure (fissura calcarina), *clc*, which, cutting deeply



into the mesial surface of the hemisphere, pushes in front of it the wall of the ventricle. In some brains in which this swelling is strongly developed its surface is somewhat indented transversely, faintly recalling a bird's claw. The lowest and least convex of the three swellings is produced by a thickening in the mass of longitudinal white fibres, fasciculus longitudinalis inferior, *Fli*. The choroid plexus does not enter the posterior horn.

The **inferior (descending) horn** (fig. 26), *Vli*, extends far forwards into the temporal lobe, but terminates about 2 cm. behind its pole. It is apparently open to the mesial surface through the hippocampal fissure (fissura cornu Ammonis, *h*). For the greater part of its extent the inferior horn is roofed in by the tapetum; the tail of the caudate nucleus and the stria cornea also extend to the front of this horn. Near the anterior end of the cornu Ammonis the tail of the caudate nucleus, which by this time is reduced to a thin grey band, begins to swell suddenly, and passes over into the nucleus amygdaleus (figs. 20 and 23).

Let us enter the inferior horn from the mesial side through the fissura hippocampi, *h*, with a view to explore its inferior wall. A succession of structures are met with, all arranged longitudinally; first, a broad convolution, gyrus hippocampi (subiculum cornu Ammonis), *H*, on the surface of which, in the fresh brain, a reticulated white layer is recognisable, substantia reticularis Arnoldi; secondly, a frequently notched grey cord, almost hidden at the bottom of a furrow, fascia dentata, *fd*; thirdly, a flattened or triangular white column, the fimbria, *Fi*, covering up the fascia dentata, which is only distinctly visible after the fimbria has been pushed aside; fourthly, a considerable white swelling, the pes hippocampi majoris (cornu Ammonis, *CAm*), which is greatly enlarged and distinctly indented in front; fifthly, in the depth of the inferior horn is to be found not infrequently a swelling, eminentia collateralis Meckelii, *EcM*, which, like the pes hippocampi minoris of the posterior horn, is simply due to the deep indentation of the surface by a fissure (fissura collateralis seu occipito-temporalis inferior), *oti*. The eminentia collateralis is separated from the cornu Ammonis by a furrow, which I will call the fissura subiculi interna, so deep that it almost splits the subiculum. It is not distinctly marked off from the tapetum on the outer side.

Of the several structures just mentioned, the subiculum and fascia dentata, as well as part of the fimbria, lie outside the inferior horn proper. The fimbria presents a sharp edge, to which the plexus choroideus lateralis, *Pc*, is attached. Only the portion of the fimbria which lies laterally to this edge enters the inferior horn. The cornu Ammonis and eminentia collateralis properly form its floor.

Followed back to the splenium corporis callosi, one sees that the subiculum cornu Ammonis is continued over the corpus callosum as the gyrus cinguli, *Cng*; also, that the fascia dentata is the termination of the free edge of the cortex. Above the corpus callosum it constitutes a thin layer of grey substance hardly distinguishable from the cortex of the gyrus cinguli, indusium griseum. The free mesial edge of the indusium is thickened, and forms (without other addition) certain recognisable longi-



tudinal striæ, striæ longitudinales mediales (*seu nervi Lancisii*, *Stlm* (fig. 22, *NL*, fig. 23). Just before the fascia dentata, having reached the splenium corporis callosi, begins (much diminished in size) to ascend on to its upper side, it swells out into a tubercle looking as if the great splenium pressed it down, tubercle fasciæ dentatæ (*Zuckerkancl*), *Tf* (fig. 22). Between this tubercle and the ascending gyrus hippocampi, and connected with the latter, lie certain minute convolutions, better seen in many animals than in Man, which *Zuckerkancl* calls callosal convolutions, *BW*. Exceptionally in Man, these convolutions form a noticeable cord-like body, which stretches on to the upper surface of the corpus callosum beneath the

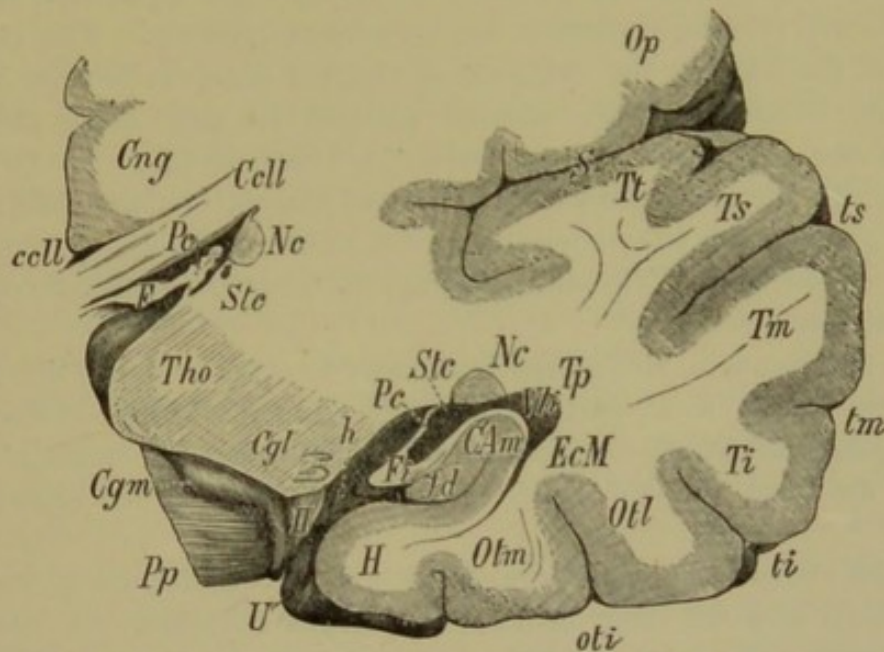


Fig. 26.—Frontal section through the right hemisphere behind the uncus. *Anterior segment.* (Natural size.)—The upper part is not represented.—*II*, Tractus opticus; *CAm*, cornu Ammonis; *Cell*, corpus callosum; *cell*, sulcus corporis callosi; *Cgl*, corpus geniculatum laterale; *Cgm*, corpus geniculatum mediale; *Cng*, cingulum; *EcM*, eminentia collateralis Meckelii; *F*, fornix; *fd*, fascia dentata; *Fi*, fimbria; *h*, fissura hippocampi; *H*, gyrus hippocampi; *Nc*, nucleus caudatus; *Op*, operculum; *oti*, sulcus occipito-temporalis inferior; *Otl*, *Otm*, gyri occipito-temporalis lateralis et medialis; *Pc*, plexus choroideus lateralis; *Pp*, pes pedunculi; *S*, fissura Sylvii; *Stc*, stria cornea; *Tho*, thalamus opticus; *Tp*, tapetum; *Ts*, *Tm*, *Ti*, gyri temporalis superior, medius et inferior; *ts*, *tm*, *ti*, sulci temporalis sup., med. et inf.; *Tt*, gyrus temporalis transversus; *U*, uncus; *Vli*, inferior horn of the lateral ventricle.

gyrus fornicatus. The fascia dentata and the nervi Lancisii, which pass over the genu corporis callosi to reach the base of the brain and there cross the substantia perforata anterior towards the temporal pole, form together an almost complete ring.

The fimbria becomes the crus fornicis, *Fcr*. The splenium corporis callosi squeezes itself in between the crus and the continuation upwards of the fascia dentata. Between these two structures and the corpus callosum a triangular area is left.

Starting at the foramen of Monro and travelling along the concave



border of the fornix, the plexus choroideus finds entrance from the mesial surface into the lateral ventricle through a curved cleft (figs. 22 and 24). Development teaches us, however, that no true gap in the brain-wall exists, for the foramen of Monro is all that is left of a much larger passage from the primary to the secondary fore-brain found in the foetus. The velum interpositum, which springs from the primitive falx cerebri, is, with its choroid plexus, developed early in foetal life. By its further growth on the two sides the velum interpositum pushes the inner walls of the primitive cerebral vesicles before its margin into their cavities (the future lateral ventricles), and so makes in each of them a cleft which arches backwards over the thalamus from the foramen of Monro; the transverse fissure of the cerebrum (*fissura choroidea seu transversa cerebri*). The involuted portion of the wall of the ventricle is thinned down to a mere layer of epithelium, which covers the choroid plexus, but still, along the whole extent of the transverse fissure, closes the ventricle in.

In fig. 24 the space between the lateral margin of the fornix and the line along which the tela choroidea is fixed to the thalamus corresponds to the transverse fissure. Through this gap the choroid plexus advances into the lateral ventricle.

[It is not common in English text-books to extend the use of the term 'transverse fissure' to all parts of the cleft through which the velum interpositum gains admittance to the lateral ventricles, but the custom is rather to limit the term to the 'transverse fissure of *Bichat*' or *incisura marsupialis*.]

Fig. 26 shows the plexus choroideus, *Pc*, in two situations, one in the inferior horn and the other beneath the corpus callosum. In this latter situation the pitting in of the wall of the ventricle by the plexus is also to be seen.

## 7. THE FISSURES AND CONVOLUTIONS ON THE SURFACE OF THE GREAT BRAIN.

The great brain may be regarded as a single almost globular body, divided by the great longitudinal fissure into two hemispheres, each of which presents a convex outer (lateral) and a flat mesial surface, which meet at an edge, sharp for the greater part of its extent.

On the surface of the adult brain a large, although variable, number of fissures are visible, besides certain structures not properly superficial, which we find in the midst of its mesial surface. Between them the surface is raised into convolutions.

It must be allowed that the fissures and convolutions of the cortex are not constant in arrangement; most of them, however, follow a definite type, and much trouble has been taken to determine the laws of their topographical distribution. We cannot yet regard the investigations into their developmental history and arrangement in different animals as complete.

In the following account, *Ecker's* nomenclature will be adopted on



the ground that, being accepted by most anatomists, and being understood in all lands, his classification has come, in a sense, to be an international one. We must bear in mind, however, that it needs considerable modification to bring it into harmony with the results of numerous attempts recently made to perfect our knowledge of the surface of the brain and to determine the true type of convolution.

The question is often discussed whether greater attention should be paid to the convolutions or the fissures. The proper way to look at the matter is to regard the fissures as cut into the surface of the brain, the convolutions as the portion of tissue left between adjoining fissures.

If an embryonic human brain is examined at the fifth or sixth month, or if we look at the brain of a rodent animal, certain fissures are seen cutting into the flat surface in regions where no convolutions have yet appeared; the latter only make their appearance as the fissures become numerous and approach near together.

Fissures may be arranged in order of importance in the three following groups:—

1. Principal or total fissures (*fissuræ*, *scissuræ*, *sulci primarii*).
2. Typical or secondary fissures (*sulci secundarii*).
3. Atypical or tertiary fissures (*sulci tertii*).

The chief fissures are the first to appear and permanently the deepest. They are called total fissures, because in early embryonic life, when the wall of the ventricle is thin, they involute it into the ventricular cavity. An example of this condition persists in the adult brain in the posterior horn of the ventricle, the calcar avis, *Phmn*, being formed in this way (fig. 25). The later subsidiary fissures sink into the surface only; they are divisible into those which are present in every normal brain (secondary fissures), and those which are subject to individual variations in number and direction (tertiary fissures).

The portions of the brain marked off by fissures are distinguished as lobes, lobules, and gyri.

The chief divisions are distinguished as lobes. This delimitation applies not to the cortex only, but also to the underlying mass of the brain. Each lobe comprises convolutions of which some in ordinary parlance are termed lobules. Typical convolutions, it goes without saying, are those bounded by typical fissures. Atypical fissures bound atypical convolutions. We only recognise as convolutions those which appear on the surface, and often forget that little convolutions are to be found in the bottom of certain fissures; deep or bridging convolutions. The superficial connections between adjoining convolutions are named by *Merkel* gyri transitori [annectant convolutions]. The amount of cortex hidden away in the fissures is in the human brain about double that which appears on the surface.

**Chief Fissures.**—1. *Fissura Sylvii* (*fossa Sylvii*,\* *fissura lateralis*), fig. 27. It is essentially distinguished from all other fissures by the

\* [A term better restricted to the open depression on the foetal brain, which precedes the closed-in fissure of Sylvius.]



manner of its origin. Its appearance is due to the fact that the great brain, during its growth, curves round its central stem-connection, making on its surface an arch open in front and below, which closes in an area, also invested with cortex, at first oval and later triangular in form, the 'island.'

During the further growth of the brain, the island is, in a sense, fixed to the stem portion of the hemisphere, while the rest of the great brain is

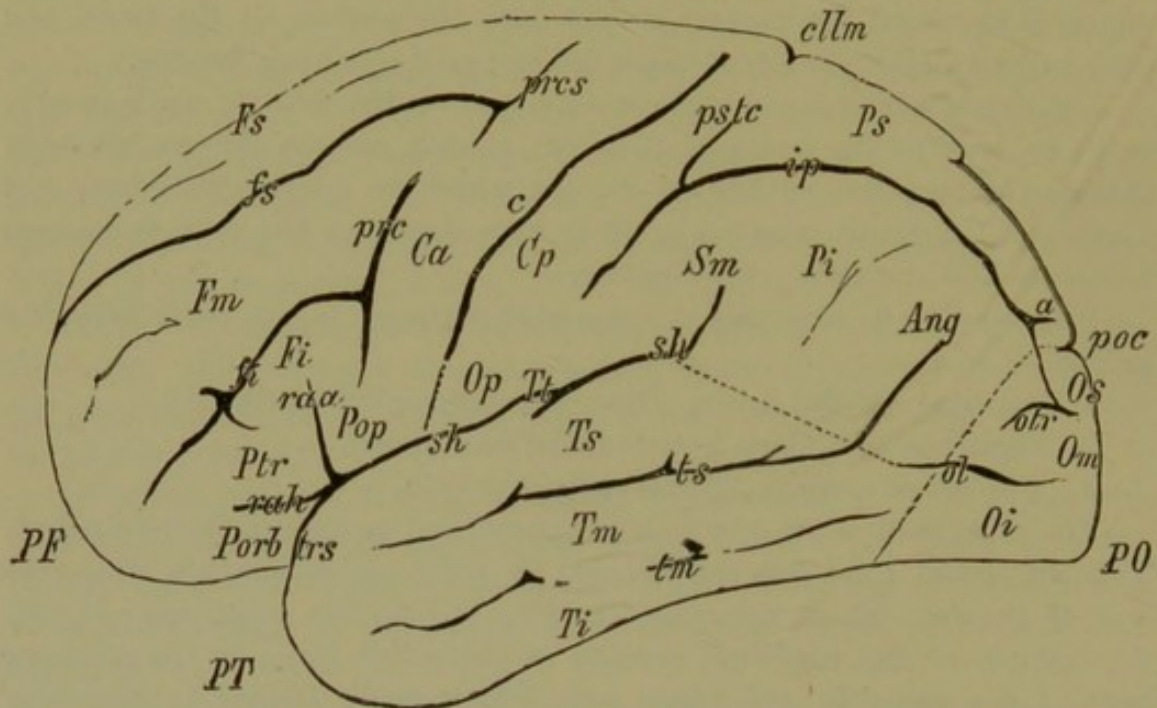


Fig. 27.—Left hemisphere from the side (*half natural size*).—*a*, Sulcus parietalis transversus; *Ang*, gyrus angularis; *c*, central fissure; *Ca*, gyrus centralis anterior; *cllm*, sulcus calloso-marginalis; *Cp*, gyrus centralis posterior; *fi*, sulcus frontalis inferior; *Fi*, gyrus frontalis inferior; *Fm*, gyrus front. medius; *Fs*, gyrus frontalis superior; *fs*, sulcus frontalis superior; *ip*, fissura interparietalis; *Oi*, gyrus occipitalis inferior; *ol*, sulcus occipitalis lateralis; *Om*, gyrus occipitalis medius; *Op*, operculum; *Os*, gyrus occipitalis superior; *otr*, sulcus occipitalis transversus; *PF*, frontal pole; *Pi*, lobulus parietalis inferior; *PO*, occipital pole; *poc*, fissura parieto-occipitalis, pars lateralis; *Pop*, pars opercularis; *Porb*, pars orbitalis; *prc*, sulcus præcentralis inferior; *prcs*, sulcus præcentralis superior; *Ps*, lobulus parietalis superior; *pstc*, sulcus postcentralis, a constant little side branch of the interparietal fissure in front of the parieto-occipital fissure; *PT*, temporal pole; *Ptr*, pars triangularis; *raa*, ramus anterior ascendens; *rah*, ramus anterior horizontalis; *sh*, pars horizontalis; *Sm*, gyrus supramarginalis; *Ti*, gyrus temporalis inferior; *tm*, sulcus temporalis medius; *Tm*, gyrus temporalis medius; *trs*, truncus fissuræ Sylvii; *Ts*, gyrus temporalis superior; *ts*, sulcus temporalis superior; *Tt*, gyrus temp. transversus. The boundaries between the four lobes when not made by fissures are marked with dotted lines.

free; hence surrounding parts bulge over the island, and, closing it in from three sides (from the front, from above, and from below), leave it lying at the bottom of a [V-shaped] cleft, the fissura Sylvii. The island is seen only after the neighbouring convolutions have been pulled aside.

The form of the Sylvian fissure is determined by this growth of the hemisphere from three sides. It consists of a short commencing portion,



*trs* (truncus fissuræ Sylvii), belonging for the most part to the base of the brain, which ascends abruptly from the substantia perforata anterior on to the lateral surface of the hemisphere, and then bends over into the principal or horizontal portion of the fissure, *sh* (ramus horizontalis posterior); this ramus runs, slightly ascending, far backwards. Two short but deep lateral fissures usually ascend from the anterior portion of the horizontal ramus; of these, the first runs horizontally forwards, *rah* (ramus anterior horizontalis); the other ascends vertically, *raa* (ramus anterior ascendens). Usually the Sylvian fissure ends by turning upwards at a somewhat acute angle. It is then called ramus posterior ascendens. A short secondary ramus is often found descending from the angle. In most brains the Sylvian fissure is decidedly longer on the left side than on the right (*Eberstaller*).

2. Sulcus centralis (sulcus Rolandi, fissura transversa), *c*. This fissure also runs its course on the convex surface. It begins at about the level of the centre of the mesial cortex-border, but without quite reaching the edge, and is thence directed obliquely forwards and downwards towards the

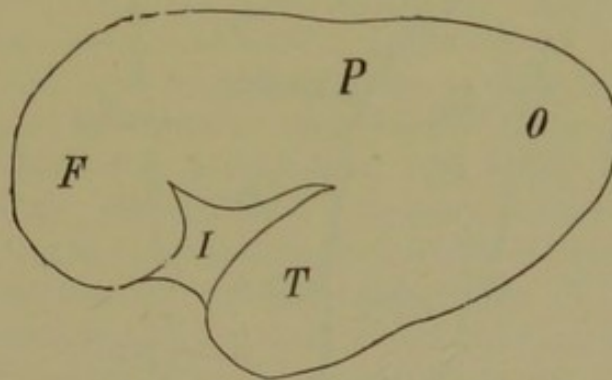


Fig. 28.—Left hemisphere of a human embryo at the fifth month.—*F*, Frontal; *P*, parietal; *O*, occipital; *T*, temporal lobes; *I*, island of Reil.

horizontal limb of the Sylvian fissure, generally making two sharp turns on the way, the superior and inferior genu of the sulcus centralis. The cases in which it extends into the Sylvian fissure amount to about 10 per cent. Since the central fissure does not cut deeply enough into the surface to produce a bulging of the ventricle wall, it ought not, strictly speaking, to be treated as a chief fissure, but its early origin, depth, and constancy justify us in assigning this rank to it.

3. Fissura parieto-occipitalis (fissura occipitalis, f. occipitalis perpendicularis), *poc*, belongs in its principal part to the mesial, in its smaller part to the lateral surface. Hence two divisions are distinguished, and often called by separate names. A mesial portion (fissura perpendicularis interna), fig. 30, and a lateral portion (upper part or fissura perpendicularis externa), fig. 29. The fissure on the mesial surface is distinguished by its depth and extent. Commencing at the cortex-border some 4 or 5 cm. in front of its posterior angle, it runs downwards and sharply forwards, joining another fissure (fissura calcarini, about to be described) at an acute angle. As already mentioned, the parieto-occipital



fissure extends over the border, and runs a short course (1 to 2 cm.) on the convex surface. Exceptionally, it reaches a long way down.

4. Fissura calcarina (fissura occipitalis horizontalis, pars posterior fissuræ hippocampi), *clc* (fig. 30), belongs exclusively to the mesial surface.

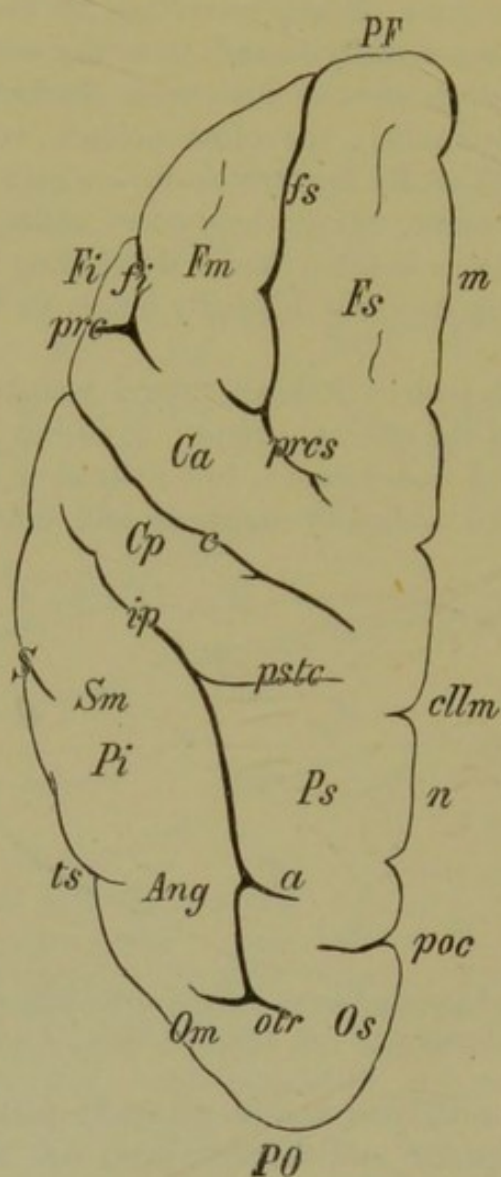


Fig. 29.—Left hemisphere from above (*half nat. size*).—*a*, Side branch of the intra-parietal fissure in front of the parieto-occipital; *Ang*, gyrus angularis; *c*, central fissure (fissure of Rolando); *Ca*, gyrus centralis ant.; *cllm*, sulcus callosomarginalis; *Cp*, gyrus centralis posterior; *fi*, sulcus frontalis inf.; *Fi*, gyrus frontalis inf.; *Fm*, gyrus frontalis medius; *Fs*, gyrus frontalis sup.; *fs*, sulcus frontalis sup.; *ip*, fissura intraparietalis; *Om*, gyrus occipitalis medius; *Os*, gyrus occipitalis superior; *otr*, sulcus occipitalis transversus; *PF*, frontal pole; *Pi*, lobulus parietalis inf.; *PO*, occipital pole; *poc*, fissura parieto-occipitalis; *pre*, sulcus præcentralis superior; *Ps*, lobulus parietalis sup.; *psc*, sulcus centralis post.; *S*, fissura Sylvii; *Sm*, gyrus supra-marginalis; *ts*, sulcus temporalis superior. The antero-posterior diameter of the corpus callosum, as it lies in the great longitudinal fissure, is indicated by the distance between *m* and *n*.

It commences near the posterior angle of the hemisphere, usually in two very short limbs, runs horizontally forwards, joins the parieto-occipital fissure, and terminates not far below the splenium corporis callosi.



Two fissures which are not to be recognised in the fully-developed brain must be added to the 'total' fissures. They bound the gyrus arcuatus, which lies on the mesial surface of the foetal brain.

1. The arcuate fissure, which in its upper portion bounds the corpus callosum (sulcus corporis callosi, *cell*, sometimes most inaptly designated *Sabatier's* ventricle), but which below corresponds to the fissure (fissura dentata) which causes the hippocampus major to bulge into the descending horn of the lateral ventricle (figs. 26 and 30, *h*).

2. Fissura choroidea, which in the developed brain is no longer obviously present, nor is it any longer in relation to the cortex proper. It is represented by the folding of the choroid plexus into the lateral ventricle already frequently mentioned.

**The Separate Lobes of the Great Brain.**—The attempt has been made to use the chief fissures as boundary lines for the lobes of the brain, but these fissures only constitute portions of such border lines, and for the rest the division must always remain an arbitrary one. The frontal lobe (lobus frontalis) is the piece in front of the central fissure and above the fissure of Sylvius. The parietal lobe (lobus parietalis) begins behind the central fissure, and reaches backwards as far as the parieto-occipital fissure and downwards to the fissure of Sylvius, but it is not completely separated by means of these fissures, either from the occipital lobe which lies behind it or the temporal lobe which lies below. Hence these boundaries are artificial, and differently understood by different authors. Remaining as far as possible true to *Ecker's* typical classification of the convolutions, we will employ, for the purpose of distinguishing the parietal from the occipital lobe, a shallow impression (*impressio petrosa*) on the under side of the hemisphere, corresponding to the upper angle of the petrous portion of the temporal bone; an impression often to be seen only just after the brain is taken from the skull. A line continuing the direction of the parieto-occipital fissure as far as this depression separates the two lobes. It is still more difficult to define the temporo-sphenoidal (*seu* temporal) lobe. From the angle made by the horizontal and ascending limbs of the Sylvian fissure we can draw a line backwards and downwards towards the fissure, which will presently be described as occipitalis lateralis (fig. 27), *ol*. Below and in front of this line lies the temporo-sphenoidal lobe.

It remains to mention the island of Reil, which lies at the bottom of the Sylvian fissure (insula Reili, lobus caudicis, *seu* intermedius *seu* opertus *seu* centralis, lobus insulæ). Its boundaries are easily defined.

The following points are to be attended to in marking out these lobes:—

The convolution lying in front of the central fissure is sometimes reckoned to the parietal lobe.

On the mesial surface the boundary between frontal and parietal lobes is not marked. Supposing the central fissure were prolonged over the border on to this surface, it would divide a small, but most characteristic, lobule (the paracentral lobule) into two parts—a similar artificial division



of the long convolution (gyrus fornicatus) which surrounds the corpus callosum would be necessary. The gyrus fornicatus is sometimes looked upon, as we shall presently see, as a special lobe.

By some (*Eberstaller* especially) it is denied that the occipital lobe reaches on the convex surface so far downwards and forwards as we have described.

It must not be forgotten that any division of the hemispheres into lobes is artificial, valuable only as a help to localising spots on its surface; we

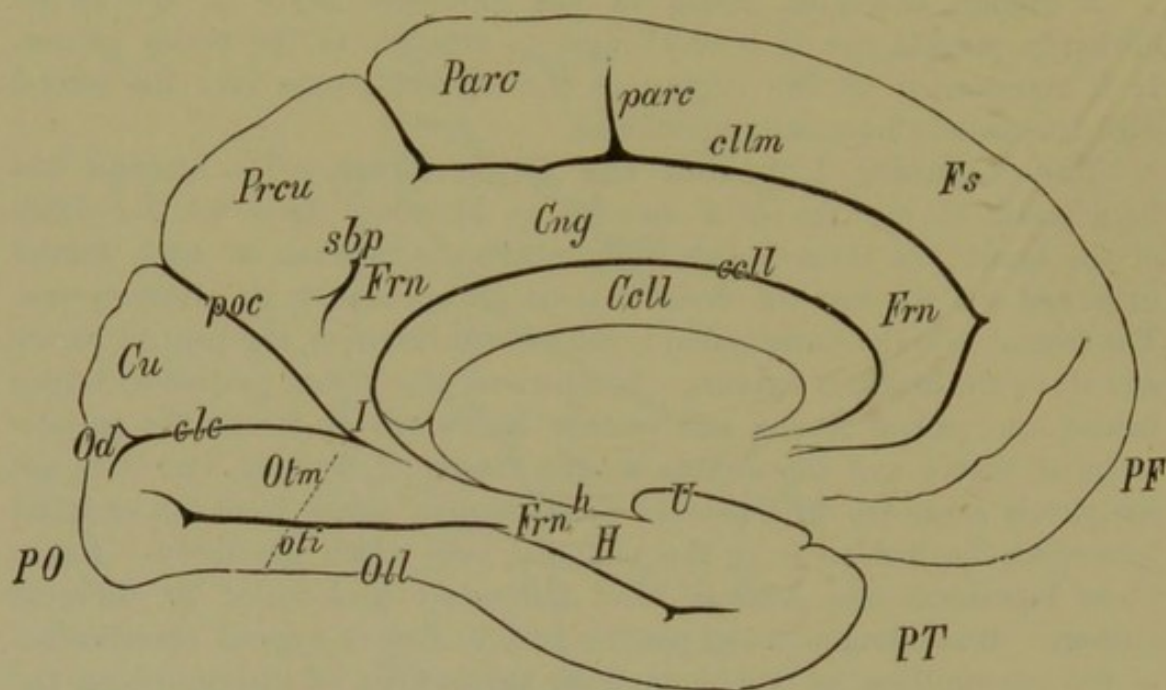


Fig. 30.—Left hemisphere, mesial surface (*half nat. size*).—*Cell*, Corpus callosum; *ccll*, sulcus corporis callosi; *cle*, fissura calcarina; *cllm*, sulcus calloso-marginalis; *Cng*, gyrus cinguli; *Cu*, cuneus; *Frn*, gyrus fornicatus; *Fs*, gyrus frontalis sup.; *H*, gyrus hippocampi; *h*, fissura hippocampi; *I*, isthmus gyri fornicati; *Od*, gyrus descendens; *oti*, sulcus occipito-temporalis inferior; *Otl*, gyrus occipito-temporalis lateralis; *Otm*, gyrus occipito-temporalis medialis; *Parc*, lobulus paracentralis; *parc*, sulcus paracentralis; *PF*, frontal pole; *PO*, occipital pole; *poc*, fissura parieto-occipitalis; *Prcu*, præcuneus; *PT*, temporal pole; *sbp*, sulcus subparietalis; *U*, uncus. The boundary between occipital and temporal lobes is shown by the dotted line, as also in fig. 27.

can easily overlook the faults which are inseparable from any method of delimitation.

[Although the classification of the lobes of the brain just discussed is highly artificial, and, like all other attempts at mapping out the brain into lobes, has no object other than to enable one to indicate with precision localities upon its surface, it yet appears to the translator that the brain during its growth exhibits a well-marked tendency to bulge into defined lobes. A survey of a large number of specimens from all the orders of mammalia leads to the conclusion that these natural lobes have a distinct morphological, and, therefore, presumably also a distinct physiological significance. As shown in the accompanying diagram, the anterior end of the cerebral hemisphere is the part which has the appearance of greatest



stability. The appearance of the fossa of Sylvius on the outer surface seems to be due to an intimate relation which exists between the nucleus lenticularis and the overlying cortex, whereby a portion of the surface, afterwards known as the island of Reil, is fixed and prevented from participating in the free growth of the rest of the hemisphere. The result of this fixation of the floor of the fossa of Sylvius is a bulging of the general surface of the hemisphere over the fossa, by which it comes at last to be covered in at the bottom of the 'fissure' of Sylvius. In its overgrowth the surface exhibits a lobar conformation. The frontal lobe swells backwards; but the growth of this region is less exuberant than that of the rest of the convex surface. The portion of the brain which surrounds the crucial or central (Rolandic) sulcus—the sigmoid gyrus of animals—the ascending frontal and parietal convolutions or operculum of Man, constitutes the most distinct of all the lobes of the brain. Examination of a large number of brains leads to the conviction that the crucial and central sulci are homologous; but the marking out of the lobe

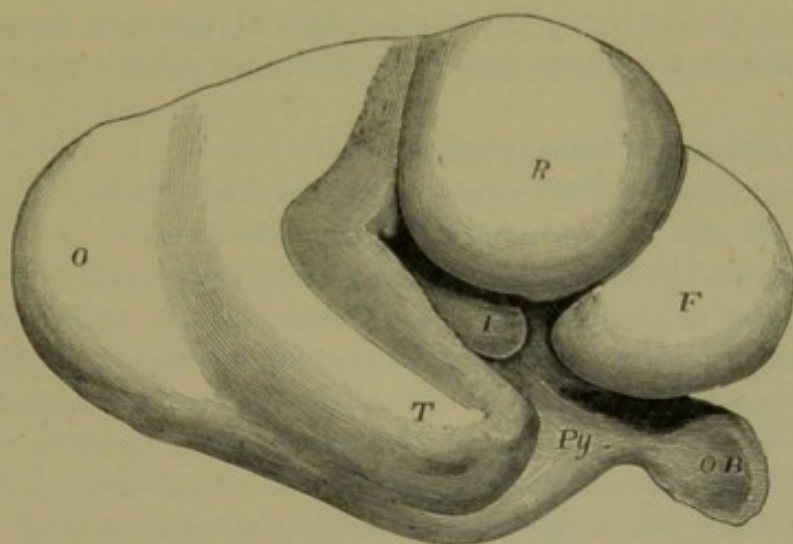


Fig. 31.—Diagram showing the lobation of the cerebrum.—*F*, Frontal lobe; *R*, Rolandic lobe; *O*, occipital lobe; *T*, temporal lobe; *I*, island of Reil; *Py*, pyriform lobe (uncinate gyrus); *OB*, olfactory bulb.

is not affected by the view taken upon this question. The sigmoid gyrus, or operculum, as it may well be called, grows downwards as a lappet which overhangs the fossa of Sylvius. The development of this lobe varies distinctly as the force, rapidity, and specialisation of movement exhibited by the animal. The inferior and posterior part of the hemisphere bulges forwards as the temporo-sphenoidal lobe, across or below the fossa of Sylvius, its position depending upon the extent to which this fossa is overhung by the lobes already mentioned. The prolongation backwards of the posterior and superior part of the hemisphere as a natural lobe is obvious in many animals. In the rabbit, for example, it assumes a rounded form, the surface between the lobe and the rest of the brain being somewhat depressed. In this respect the brain of the rabbit contrasts remarkably with that of the mole. These four bulgings, frontal,



opercular, occipital, and temporo-sphenoidal, are the largest and most distinct, but they include other less obvious elevations. It is very difficult to say how that portion of the surface which lies behind the Rolandic and temporo-sphenoidal and in front of the occipital lobe should be allocated, although there are sufficient indications of the existence upon it of other less pronounced swellings.

Undoubtedly, the fissures are morphological landmarks. They are fixed in position in relation to the tissue by which they are surrounded; but they are not necessarily divisions between regions of different function. More probably they are centres of functional areas, *e.g.*, the fissure of Rolando, the centre of the motor region; the calcarine fissure, the centre of the visual sphere, etc. Each region of the cortex, in which a variable function is localised, is liable to variations in size (*cf.* figs. 165, 166, 167).]

**1. Frontal Lobe.**—Three surfaces are to be distinguished—lateral, mesial, and basal. Since the basal surface lies on the roof of the orbit, it is often termed ‘orbital.’ Three constant fissures are found on the lateral surface:—

(1) Sulcus præcentralis, *pre* + *pres*, fig. 27 (vertical frontal fissure, sulcus prærolandicus), lies in front of and almost parallel with the central fissure.

(2) Sulcus frontalis superior, *fs*; and

(3) Sulcus frontalis inferior, *fi*, runs forwards from the præcentral sulcus, parallel with the inner border of the hemisphere.

The præcentral sulcus, which begins a short distance above the Sylvian fissure, does not, as a rule, reach so far as the posterior end of the superior frontal fissure; a short fissure, *pres*, running in the same direction, is, however, always to be found at the hinder end of the superior frontal fissure, and it may be regarded as the continuation upwards of the præcentral, which is then divided into two, sulci præcentrales inferior et superior. Usually the superior præcentral fissure runs a little downwards as well as upwards from the superior frontal.

Four convolutions are marked out by these fissures:—

(1) Gyrus centralis anterior, *Ca* (ascending frontal, præcentral, premier pli ascendant); a convolution which, running parallel with the central fissure, of which it forms the anterior boundary, traverses the whole of the lateral surface of the hemisphere from the fissure of Sylvius upwards. From it there extend forwards—

(2) Gyrus frontalis superior, *Fs* (upper, first, or third (*Meynert*), frontal convolution, gyrus frontalis marginalis).

(3) Gyrus frontalis medius, *Fm* (middle or second frontal convolution).

(4) Gyrus frontalis inferior, *Fi* (inferior, third, or first (*Meynert*), frontal convolution, pli surcilier; *on the left side only*, Broca's convolution). [The region of the cortex, injury to which produces aphasia, was localised by Broca as the back of this convolution on the left side at its junction with the ascending frontal.]

The superior frontal convolution includes the border of the hemisphere, for it extends over on to the mesial surface. Its lateral surface is often,



like that of the gyrus frontalis medius, complicated with a number of shallow inconstant fissures. The upper and lower portions of the wide anterior surface of the gyrus frontalis medius are usually divided by an uninterrupted fissure, the sulcus frontalis medius of Eberstaller, which runs parallel to the two frontal fissures. Marchand gives the name of 'oblique fissure,' sulcus frontalis obliquus, to the anterior and most deeply cut part of it. A transverse part of the same variable fissure on the border of the orbit corresponds probably to Wernicke's sulcus fronto-marginalis.

The inferior frontal convolution running forwards from the lower end of the ascending frontal winds round both the anterior ascending and the anterior horizontal limbs of the fissure of Sylvius. Hence it is divided into three parts—(a) pars opercularis, *Pop*, between the sulcus præcentralis and the ramus ascendens fissuræ Sylvii, usually divided by a diagonal fissure, sulcus diagonalis operculi, into two equal parts, one lying behind the other; (b) pars triangularis, *Ptr* (cap de la circonvolution de Broca), between the ascending and anterior horizontal rami; (c) pars orbitalis, *Porb*, in front of the horizontal ramus; this latter properly belongs to the orbital surface of the frontal lobe.

'Connecting-convolutions' between the several frontal convolutions commonly complicate the survey.

All three frontal convolutions are continued on to the orbital surface of the lobe; although the inferior frontal fissure hardly ever reaches, without interruption, on to the orbital surface, as shown in fig. 35. Here the arrangement of fissures and convolutions is very inconstant (fig. 32). It often happens that the superior (here mesial) and inferior (here lateral) frontal convolutions run backwards as far as the anterior perforated space, *Spa*, where they are united together by a connecting piece. The middle convolution is thus shut off from the perforated space by the folding together of the other two. All the fissures on the orbital surface unite together to form an H or an X, sulcus cruciatus, *cr* (orbitalis, cruciformis, triradiatus). A straight fissure which runs parallel with the great horizontal fissure is always to be seen on the orbital portion of the superior frontal convolution. In this lies the olfactory tract. It is termed, therefore, the olfactory fissure (*seu* sulcus rectus), *olf*.

It is quite unjustifiable to look upon the orbital surface of the frontal lobe as a lobe proper (lobus orbitalis). The mesial surface of the frontal lobe is better described later on, in connection with the mesial surface of the other lobes.

The most anterior point of the frontal lobe is termed the frontal pole, *PF*.

**2. Parietal lobe** presents a lateral and a mesial surface, of which only the former will be considered now. A single typical fissure indents this lobe, the intraparietal, *ip*, fig. 27 (sulcus parietalis, fissura parietalis cum f. paroccipitalis of *Wilder*). It commences behind the central fissure and above the fissure of Sylvius. At first it ascends parallel to the central fissure; it then sweeps backwards in a great curve, and finally crosses the imaginary boundary between the parietal and occipital lobes to end in the



latter. A continuation of its first portion ascends parallel to the central fissure towards the border of the hemisphere, which it does not, however, reach; so that, in a sense, a third transverse fissure is formed (the sulci præcentralis et centralis being the other two), which may be called the sulcus centralis posterior (*seu* postrolandicus), *pstc*. Interruptions to the course

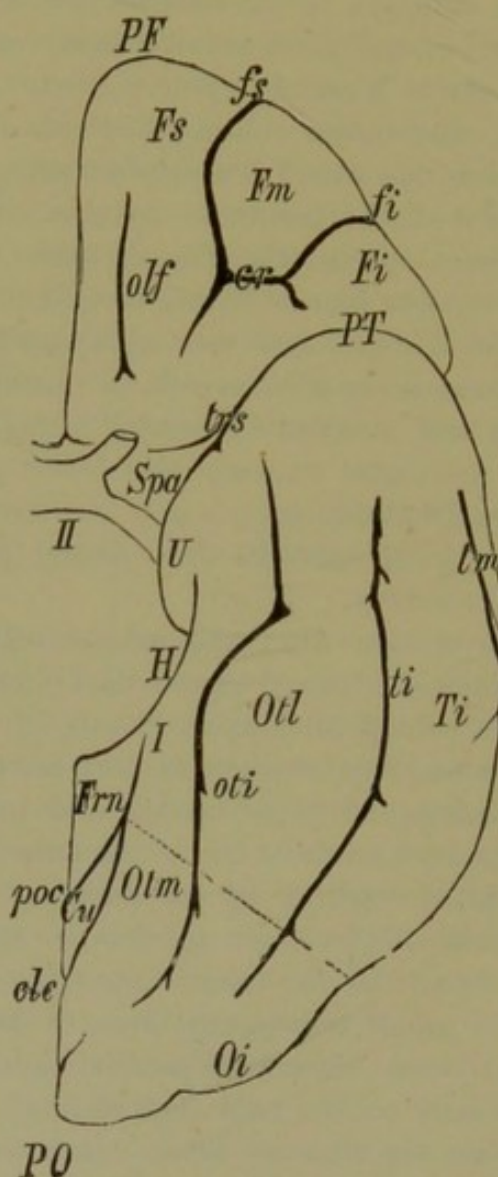


Fig. 32.—Left hemisphere from the base (*half nat. size*).—II, Chiasma nervorum opticorum; *cle*, fissura calcarina; *cr*, sulcus cruciatus; *Cu*, cuneus; *Fi*, gyrus front. inferior; *fi*, sulcus frontalis inferior; *Fm*, gyrus front. medius; *Frn*, gyrus fornicatus; *Fs*, gyrus frontalis superior; *fs*, sulcus frontalis superior; *H*, gyrus hippocampi; *I*, isthmus; *Oi*, gyrus occipitalis inferior; *olf*, sulcus olfactorius; *oti*, sulcus occipito-temporalis inferior; *Otl*, gyrus occipito-temporalis lateralis; *Otm*, gyrus occipito-temporalis medialis; *PF*, frontal pole; *PO*, occipital pole; *poc*, fissura parieto-occipitalis; *PT*, temporal pole; *Spa*, substantia perforata anterior; *Ti*, gyrus temporalis inf.; *ti*, sulcus temporalis inferior; *tm*, sulcus temporalis medius; *trs*, truncus fissurae Sylvii; *U*, uncus.

of the intraparietal fissure are very common, especially on the right side. In one-fourth of the total number of cases the most important interruption is found in the backward curve, isolating the sulcus postrolandicus. A short lateral branch (sulcus parietalis transversus), *a*, which passes towards



the border of the brain, running at the same time backwards, in front of the parieto-occipital fissure, is almost constant. Another fissure, the sulcus intermedius (*Jensen*), starts usually from the concave side of the intraparietal fissure, from which, however, it is sometimes separate, as in fig. 27, *Pi*.

Three convolutions are to be distinguished in the parietal lobe:—

(1) Gyrus centralis posterior, *Cp* (ascending parietal, postrolandicus, deuxième pli ascendant), is bordered in front by the central fissure. Around the upper end of this fissure it becomes continuous with the anterior central convolution with which it has been running parallel. Its upper part is usually narrow, and therefore markedly different from the broad upper part of the anterior central convolution.

(2) Gyrus parietalis superior, *Ps* (lobulus parietalis superior, præcuneus, gyrus parietalis primus), is that portion of the parietal lobe which lies behind the posterior central convolution and above the intraparietal fissure. It extends over the border of the hemisphere on to the mesial surface. This portion of the convolution is known as præcuneus, *Prcu*, fig. 33.

(3) Gyrus parietalis inferior, *Pi*, fig. 27 (lobulus parietalis inferior, lobulus tuberis, gyrus parietalis secundus), lying beneath the intraparietal fissure, skirts around the hinder end of the Sylvian fissure (this portion is called the supramarginal gyrus, *Sm*), and then in a similar manner encloses the superior temporal fissure which lies below and parallel to the Sylvian fissure. This second portion of the inferior parietal lobule is known as the gyrus angularis (pli courbe), *Ang*. The sulcus intermedius forms the boundary line between the gyrus supramarginalis and the gyrus angularis. The inferior parietal convolution is by no means sharply bounded on its occipital side. [There is no other part of the hemisphere the definition of which, as a whole, and its division into parts is so difficult as the inferior parietal lobule. Either of its constituent convolutions may be cut into two by the fissure which it normally confines. Supramarginal and angular convolutions may be simple, as in fig. 27, or folded so much that their outline is difficult to trace.]

The inferior frontal convolution, with the exception of its orbital portion, together with the united lower ends of the two central convolutions and the inferior parietal, so far as it lies over the island of Reil, constitute the operculum, *Op* (strictly speaking, the operculum insulæ), see p. 108. If the operculum be lifted up, or a frontal section made through the brain, it is seen that its deep surface, which looks towards the fossa Sylvii and the temporo-sphenoidal lobe, is marked by several inconstant fissures.

The mesial surface of the temporal lobe will be described later on.

**3. The Occipital Lobe.**—The occipital lobe has on the whole the form of a three-sided pyramid with its base resting upon the parietal and temporo-sphenoidal lobes, and its apex projecting as the occipital pole, *PO*. Hence we have to distinguish three surfaces, lateral, mesial, and basal. At present the lateral only will be dealt with.



The fissures on the lateral surfaces are very inconstant, the following being more easily found than the rest:—

(1) Sulcus occipitalis transversus, *otr* (hinder transverse portion of the intraparietal fissure). It lies behind the parieto-occipital fissure, and is, as a rule, continuous with the intraparietal. It runs transversely across the occipital lobe for a variable distance, and is to be regarded as the analogue of the conspicuous fissure which occupies this situation in the monkey's brain. It is sometimes altogether absent.

(2) Sulcus occipitalis lateralis, *ol* (sulcus occipitalis longitudinalis inferior). The fissure looks as if it were the prolongation backwards of the principal portion of the upper temporal fissure. It lies in the line which this fissure would follow if prolonged backwards, on the lower part of the occipital lobe, nearly to the occipital pole. *Eberstaller* looks upon it as the inferior boundary of the occipital lobe.

Three not always equally well-defined convolutions converge towards the occipital pole—

(1) Gyrus occipitalis superior, *Os* (gyrus occipitalis primus seu parieto-occipitalis medialis).

(2) Gyrus occipitalis medius, *Om* (seu secundus).

(3) Gyrus occipitalis inferior, *Oi* (seu tertius, seu temporo-occipitalis).

The superior occipital passes into the superior parietal convolution through the medium of a connecting convolution which curves round the lower end of the parieto-occipital fissure (gyrus paroccipitalis of *Wilder*, premier pli de passage of *Gratiolet* [first annectant convolution of *Turner*]). The middle convolution is the continuation of the gyrus parietalis superior (gyrus angularis). The inferior occipital ends by joining with the middle, and in part also with the inferior temporal convolution.

**4. The Temporal Lobe.\***—It presents a lateral and an inferior surface which are continuous with one another around the outer margin of the brain. Four fissures, all sagittal in direction, are to be distinguished. From the Sylvian fissure downwards they are as follows:—

(1) Sulcus temporalis superior, *ts* (parallel fissure [superior temporo-sphenoidal fissure], sulcus temporalis primus), a very constant and obvious fissure. Its chief portion, portio horizontalis, is directed straight backwards towards the occipital lobe; its hinder end, portio ascendens, which turns upwards, is surrounded by the gyrus angularis.

(2) Sulcus temporalis medius, *tm* (sulcus temporalis secundus), very often interrupted by bridging convolutions.

(3) Sulcus temporalis inferior, *ti* (seu tertius).

(4) Sulcus occipito-temporalis inferior, *oti* (inferior longitudinal fissure, fissura collateralis).

Of these four the two first are visible on the lateral surface of the brain; the remaining two belong to its under surface.

The convolutions on the lateral surface are arranged in three parallel

\* In English text-books usually termed temporo-sphenoidal lobe, a somewhat cumbrous appellation.



folds like those of the frontal lobe, only more simply. In front, at the tip of the temporo-sphenoidal lobe (*extremitas temporalis*, temporal pole, *PT*), these three convolutions, as well as some of those which lie on the under surface, unite in a rounded dome.

(1) *Gyrus temporalis superior*, *Ts* (*gyrus inframarginalis*, parallel convolution, *gyrus temporalis primus*). This convolution forms the lower boundary of the Sylvian fissure; it is continued behind into the inferior parietal lobule.

If the lobes of the brain are pulled apart, so that a view is obtained of the fossa Sylvii in all its depth, it will be seen that, just as in the case of the under side of the operculum, so also with regard to the upper surface of the temporo-sphenoidal lobe (figs. 19 and 20), a considerable portion of cortex, hitherto hidden in the fissure, is brought to light. Three, and even in some cases four, convolutions are thus exposed. They originate in the superior temporal convolution and converge backwards towards the hinder angle of the island of Reil. The most constant and longest of these gyri temporales transversi (*Heschl*) is the anterior, *Tt* (fig. 19).

(2) *Gyrus temporalis medius*, *Tm* (*seu secundus*).

(3) *Gyrus temporalis inferior*, *Ti* (*seu tertius*), forms the transition from the lateral to the under surface of the temporal lobe.

(4) *Gyrus occipito-temporalis lateralis*, *Otl* (*gyrus seu lobulus fusiformis*), lying between the sulcus temporalis inferior and the sulcus temporo-occipitalis inferior, is usually broadest in the middle, and, therefore, more or less spindle-shaped. It can almost always be followed as far backwards as the occipital pole, hence it is also an essential constituent of the under surface of the occipital lobe.

(5) *Gyrus occipito-temporalis medialis*, *Otm* (*gyrus seu lobulus lingualis*), between the inferior occipito-temporal and the calcarine fissures, forms part of the mesial and under surface of the hemisphere. It should be looked upon as belonging to the occipital lobe alone.

**The Mesial Surface of the Hemisphere.**—On this surface the arched form of the hemisphere is most conspicuous, not only in the arrangement of the whole structure, but also in the configuration of its several constituents.

The sagittal section of the corpus callosum, *Ccll*, fig. 33, has the form of an arch, around which curves a convolution which commences beneath the rostrum of the corpus callosum on the frontal portion of the mesial aspect. It is continued backwards over the corpus callosum, from which the sulcus corporis callosi, *ccll*, divides, passes beneath the splenium, and runs forwards even as far as the apex of the temporo-sphenoidal lobe. This convolution is the gyrus fornicatus, *Frn*. It is separated from the corpus callosum by the sulcus corporis callosi, *ccll*. It comprises two portions—(1) the part lying close to the corpus callosum, *gyrus cinguli*, *Cng* (*gyrus corporis callosi*, *circonvolution de l'ourlet*, *première convolution limbique*; often this portion alone is reckoned as *gyrus fornicatus*); and (2) a free-lying portion, *gyrus hippocampi*, *H* (*subiculum cornu*



Ammonis, gyrus uncinatus, seconde convolution limbique). The portion of the gyrus fornicatus in which these two segments are united is strikingly constricted, *I*, isthmus gyri fornicati. Here the middle occipito-temporal convolution, *Otm*, becomes superficial, while another constituent of the mesial surface of the hemisphere, the cuneus, *Cu*, is insinuated between it and the gyrus fornicatus. It is connected with the latter by the stalk of the cuneus, *PCu*, fig. 22 (pedunculus cunei). The gyrus hippocampi swells out considerably at the anterior part of the temporo-sphenoidal lobe, forming a hook-like curve, *U* (uncus, gyrus uncinatus). The inner boundary of the arch which forms the gyrus fornicatus corresponds approximately with the embryonic sulcus arcuatus [of *Arnold*]. It is represented in the region of the gyrus cinguli by the sulcus corporis callosi, *ccll*; in its lower portion it corresponds to the fissura hippocampi, *h*.

The fascia dentata and nervi Lancisii should be included in this enumeration as an atrophied convolution.

*Broca* describes the gyrus fornicatus (with addition of the olfactory tract) as a special lobe, lobus limbicus or rhinencephalon. Similarly *Schwalbe*, on genetic grounds, institutes his lobus falciformis, which comprises the gyrus fornicatus, septum pellucidum, and fascia dentata.

[In all animals, the lower and anterior part of the hemisphere is distinguished from the rest of the cortex-covered cerebrum by a profound difference in appearance. The roundly-swelling convoluted part of the hemisphere terminates at the rhinal fissure. The portion of the hemisphere below this fissure, known as the pyriform lobe, is flatter than the rest, indented by blood-vessels, but not fissured, and usually whiter in colour. In front it tapers off into the olfactory tract and bulb. Behind, it suddenly narrows into the gyrus fornicatus, or first convolution embracing the corpus callosum. The size of the pyriform lobe varies as the development of the olfactory apparatus. On the other hand, the extent to which it is overlapped by the temporal lobe depends upon the size of the latter, which is large in osmatic, small in anosmatic, animals. In Carnivora the temporal lobe projects far forwards over the pyriform, the rhinal fissure being bent at an acute angle. In Herbivora the rhinal fissure is almost straight, and the pyriform lobe is exposed on the lateral surface of the hemisphere. In Man, although this broad anatomical distinction between the pyriform lobe and the rest of the hemisphere is not visible, it is easy to recognise in the uncinate (including the gyrus hippocampi) the pyriform lobe of animals. The extreme anterior end of the gyrus fornicatus, the "terrain désert" of *Broca*, resembles to some extent the gyrus uncinatus in its superficial aspect, and is also connected, apparently, with one of the roots of the olfactory tract. It was quite unjustifiable, however, to introduce the gyrus fornicatus into the connection, making one large "lobe limbique" in the "form of a racquet," since the ground upon which this was done, the supposed connection of the limbic lobe with the sense of smell, is at once shown to be untenable by the fact that in animals in







tinued by a shallow depression or an inconstant fissure, sulcus subparietalis, *sbp*.

Apart from the gyrus fornicatus and fascia dentata a number of different named areas are met with on the mesial surface of the hemisphere, commencing at the frontal end:—

1. Gyrus frontalis superior (here called also circonvolution frontale interne), *Fs*. The first part of it a wide area lying beneath the genu corporis callosi, is invariably cleft by a longitudinal fissure, sulcus infra-orbitalis inferior.

2. The loop of communication between the upper ends of the two transverse convolutions, lobulus paracentralis, *Parc*, which reaches backwards to the ascending portion of the sulcus calloso-marginalis, while its anterior boundary is formed by the sulcus paracentralis.

3. Præcuneus, *Prcu* (lobulus quadrata, mesial surface of the gyrus parietalis superior), is a plump four-sided piece of cortex, of about the same size as the lobulus paracentralis, which extends as far backwards as the internal parieto-occipital fissure. A fairly constant shallow fissure, sulcus parietalis transversus (*Brissaud*), running up from the sulcus subparietalis, divides the anterior and posterior halves of the præcuneus.

4. The cuneus, *Cu* (lobulus triangularis, mesial surface of the gyrus parietalis superior, a conspicuous triangular portion of the cortex lying between the parieto-occipital and calcarine fissures. The front of the wedge runs forwards as far as the isthmus fornicatus. It is known as the pedunculus cunei, *PCu* (*cf.* fig. 33).

5. The gyrus occipitalis descendens, *Od*, is seen as a narrow convolution lying behind the bifid end of the calcarine fissure near the occipital pole. It unites the cuneus with

6. The gyrus occipito-temporalis medialis, *seu* lingualis, *Otm*. Beginning at the occipital pole as a very broad convolution, it passes forward, narrowing as it goes, and joins the gyrus hippocampi beneath the splenium corporis callosi. It occupies the greater part of the basal surface of the occipital lobe. Another part of it belongs to the mesial surface. It is divided into two segments by a constant longitudinal fissure, sulcus gyri lingualis.

**The Island of Reil.**—This region is hidden by other portions of the hemisphere which grow over it from three sides, the three opercula (*O. fronto-orbitale, seu ant., O. parieto-frontale, seu sup., O. temporale, seu post.*; the first two are often called the operculum). The result is, that the island assumes the form of a triangular pyramid, the base of which rests on the brain-stem, while its apex (pole of the island of Reil, the point on its surface which projects farthest laterally) is cut off from the rest of the cortex by the sulcus circularis Reili. It is only wanting in front and on the ventral side, where the island is continuous with the lamina perforata anterior (limen insulæ), *trs* (fig. 32). The island is divided by a constant fissure, sulcus centralis insulæ, which runs from the limen insulæ upwards and backwards, almost parallel with the sulcus Rolandi, into a larger anterior (pars frontalis) and a smaller posterior



part (*pars parieto-occipitalis*). Both parts are split up into a number of convolutions, *gyri recti* (*seu operti, seu breves insulæ*), by secondary fissures, which run in the same general direction. *Eberstaller* restricts the name of *gyri breves* to the three or four convolutions of the anterior part, all of which (except the most anterior) converge and unite at the pole of the island. The longer convolutions of the posterior part, usually two in number, pass downwards to the temporal pole. Between them lies the sulcus post-centralis Reili (*Cunningham*). According to *Marchand* this is the first permanent fissure of the island of Reil, and is distinguishable in the embryo at the end of the seventh month.

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The simple arrangement of convolutions described above is usually masked by the presence of numerous atypical furrows and convolutions; hence it is often difficult for an inexperienced observer to find his way about the surface of the hemisphere and pick out the typical convolutions from the apparent chaos. The first fissure to look for is always the Sylvian, which cannot be confused with any other. Next the central fissure [of *Rolando*] is found. In looking for this a mistake might in the first moment be made. A good guide, however, is afforded by the posterior transverse convolution rapidly narrowing in its upper part and bounded at the top by the portion of the calloso-marginal fissure which turns over on to the lateral surface. If now the parieto-occipital fissure is found as it turns over the border of the hemisphere, a sufficient number of starting-points are determined to enable the student to orient the rest of the surface.

The beginner is strongly recommended to study the convolutions and fissures in as many brains as possible, in order that he may learn to recognise them quickly. As long as the surface is covered by pia mater the fissures are extremely difficult to find.

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#### VARIETIES AND ANOMALIES OF CONVOLUTION.

We have so described the principal and chief subordinate fissures as to make it possible to find them with more or less ease in any normal brain.

Non-essential differences in the arrangement of the primary and secondary fissures, as well as wide variations in the course of the tertiary fissures, characterise individual brains. There are always differences between the two hemispheres, and the richer the brain in convolutions the greater is the difference between its two sides. Similar individual variations in the arrangement of the convolutions in different individuals and differences between the two hemispheres are found in animals. In them, too, variation increases with development.

The form of the skull is of great importance in determining the type of brain-convolution. In dolichocephalic heads the brains incline



towards an exaggeration of the longitudinally arranged convolutions and fissures, while in people with brachycephalic skulls the transverse fissures and convolutions are dominant. Early synostosis alters the arrangement of the convolutions in a similar manner (*Zuckerkandl*).

For the oft attempted determination of racial types (if any there be which are not due merely to the typical skull-conformation) the data before us are as yet wholly insufficient.

One is often tempted to assert that complexity in convolution keeps pace with intellectual power; such a connection is not, however, demonstrable in every individual case. Often it seems possible to recognise a conspicuous development of convolutions to which a definite physiological purpose can be assigned in individuals remarkable for the preponderance of the corresponding faculties.

The best example of this is the inferior frontal convolution of the left side, which is in intimate connection with the faculty of speech. *Rüdinger* asserts that in the brains of great orators this convolution is strongly developed; in the otherwise exceptionally small brain of Gambetta,\* the pars triangularis was large, strongly twisted, and, in a certain sense, doubled (*Duval*). On the other hand the pars opercularis may be so slightly developed, that a portion of the island of Reil is uncovered and exposed from the surface. Great pains have been taken to discover a difference in type of convolution in the two sexes, but only slight and inconstant differences have been discovered (*Huschke*, *Wagner*, *Rüdinger*). It has been pointed out that the frontal lobe is better developed in the male. *Passet's* assertion that the sulcus centralis is longer in the male is contradicted by *Cunningham*. *Eberstaller* has proved by careful measurements that the fissura Sylvii is somewhat longer in the female brain.

All the principal fissures are present in human brains at the time of birth, but secondary and tertiary fissures are still some time from their complete development (only a month according to *Sernoff*). The relation of the fissures to one another changes during the growing period, some parts of the brain developing quickly, others lagging behind. The measurement and comparison of the angle, in front, which the two central fissures make with one another, has led to conflicting conclusions (*Cunningham*).

If, as the result of senile marasmus, or owing to other causes (chronic mental disease, for example), atrophy of the brain sets in, the convolutions become narrower, the fissures broader. Extreme atrophy of single convolutions, probably consequent upon intra-uterine disease, is known as microgyry. In tumours or rare cases of hypertrophy of the brain, the convolutions are pressed up against the bones of the skull and flattened. When the brain, though not actually hypertrophied, is unusually large, we find the convolutions remarkably broad. Small brains, on the other hand,

\* [The report which went the round of the newspapers at the time of Gambetta's death that his brain was phenomenally small, weighing no more than 1,100 grms., seems to have been a complete mistake. *Duval's* estimate of 1,241 grms has been confirmed by *Rüdinger* and others.]



produce the impression of being singularly rich in fissures, on account of the smallness of the spaces between.

When the fissures are conspicuously increased, although they are only superficial, the condition is known as polygyry. Occasionally little knobs of cortical substance project from the surface of convolutions, especially the superior frontal.

The frequency of **anomalies in convolution** is variously estimated; some people describing as an anomaly what is only regarded by others as a variation.

For example, it cannot be properly regarded as an anomaly when the central fissure, which originates in two parts (*Cunningham*), is divided into an upper and a lower half owing to the exceptional development of a convolution which is almost always present as the remnant of the embryonic bridging convolution (the posterior prolongation of the middle frontal convolution), although out of sight. The anterior central convolution is not rarely interrupted (especially in the upper half) by a fissure, more or less deeply cut. It may be present in both hemispheres. The sulcus postcentralis or the anterior end of the sulcus intraparietalis not unfrequently cuts into the Sylvian fissure, but the communication thus established is purely superficial. We also not unfrequently find the calcarine fissure bridged over by a convolution; in many cases this occurs twice in its course (*Richter*).

Anomalies, in the strict sense of the word, are extremely rare. They usually accompany congenital deficiency of intellect, such as idiocy or epilepsy. Many attempts have been made, not always with success, to discover in these deviations from the normal a reversion to the animal type of brain (especially as observed in monkeys).

More striking anomalies of the brain-surface are found as purely teratological conditions; for example, cyclopia, associated in microcephalic brains, with absence of certain parts, as, for example, the corpus callosum, the occipital lobes (inoccipitia, *Richter*), or the olfactory lobes (arrhinen-cephalia, *Kundrat*). Also as the result of certain destructive pathological processes occurring either in intra- or extra-uterine life; for example, in porencephalia a certain portion of the surface of the brain is absent, and the ventricle is only separated from the surface by the meninges. A very rare, but interesting, anomaly in the arrangement of the convolutions, is that condition in which the two hemispheres are not completely separated from one another, but certain convolutions bridge across the great longitudinal fissure (*Hadlich, Wille, Kundrat, Arnold, Turner*).

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#### PHYSIOLOGICAL MEANING OF THE CONVOLUTIONS.

Our exact knowledge of the topography of the cortex has been acquired since the time when it was first realised that the different regions into which it is divided are endowed with separate functions. Some physiologists still either disbelieve in **localisation** or only allow the application



of the law in a modified sense; but a long series of successful clinical diagnoses now place beyond the reach of contradiction the fact that certain regions of the cortex are to a greater extent than the rest associated with certain functions. Unfortunately the facts elicited by clinical observation are not in full accord with the results of experiment. A full agreement as to the division of functions in the cortex does not yet obtain amongst the followers of the localisation theory, on which account we shall content ourselves with stating those points which may be considered as definitely settled. We shall take our stand upon a moderate localisation, such as was first enunciated by *Exner*.

Individual centres and cortex-fields are not to be considered as sharply outlined and definitely marked off from neighbouring regions; the so-called centres are rather the spots of maximal relation to functions which fade away into neighbouring areas. Hence it follows that the cortex-fields to a certain extent overlap one another.

In the following summary we shall speak of the centres in this sense as comprehending the spots of maximal physiological relation.

The functions of the gyrus frontalis superior and medius are not sufficiently well known. Attempts have often been made to associate them with the higher psychical function "intelligence"; but no satisfactory proof of this theory has yet been adduced. They suffer most in dementia paralytica. It is, however, certain that intellectual functions result from the combined action of the separate but intimately connected regions of the cortex. It should be strongly insisted on that no structural cause has been discovered for those higher psychical processes which lie beyond the simple processes of sensation and movement. The gyri frontalis inferior, centrales anterior et posterior, the lobulus paracentralis, and the anterior part of the superior parietal lobule, together constitute the motor region (motor-field or sphere). Here the motor activity of the cortex is localised to the greatest extent; it chiefly controls the muscles of the opposite side of the body; to a subordinate degree those of the same side also. The question of whether its influence is exercised by direct or reflex action is one upon which I shall not enter here.

The centres of muscle-sensibility are probably to be found in this region.

The groups of muscles represented in this region may be classified as follows:—

Tongue muscles (11, fig. 34)—lowest part of the gyrus centralis anterior.

Mouth muscles (12)—immediately above the tongue muscles.

Face muscles (13, 14)—inferior portion of the gyrus centralis anterior (and posterior?), all but the lowest part.

Larynx muscles (9) (particularly those which subserve phonation)—lowest part of the gyrus frontalis inferior where it passes over into the gyrus centralis anterior (?).

Muscles of the upper extremity—middle part of the gyrus centralis anterior extending over on to the gyrus centralis posterior, probably in the



following order from below upwards: thumb (7), forefinger (6), other fingers (5), wrist (4), elbow (3), shoulder (2).

Muscles of the lower extremity—upper part of both gyri centrales, lobulus paracentralis, and perhaps the anterior part of the gyrus parietalis superior; probably in the following order from before backwards: hip-joint (20), knee (21), ankle (22), great toe (23), other toes (24).

A safe localisation of the remaining voluntary muscles is not yet possible. *Schäfer* and *Horsley* are of opinion that the muscles of the

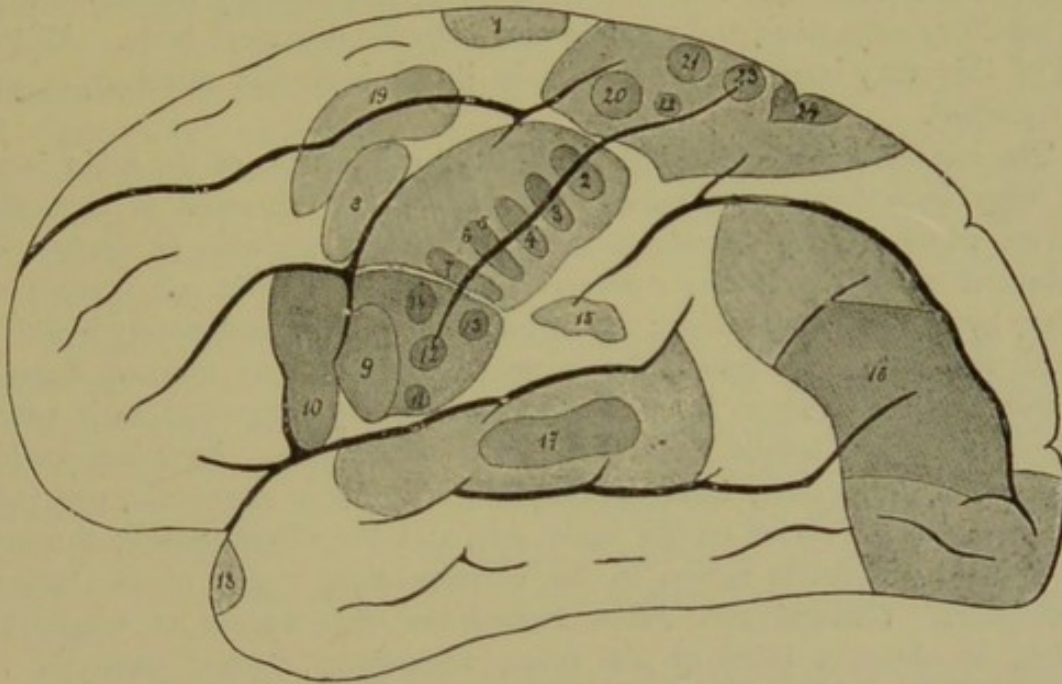


Fig. 34.—Cortical localisation according to *Debord* and *Achard*. 1, trunk; 2, shoulder; 3, elbow; 4, wrist; 5, three last fingers; 6, forefinger; 7, thumb; 8, agraphia; 9, larynx; 10, motor aphasia; 11, tongue; 12, mouth; 13, lower facial; 14, upper facial; 15, eye muscles; 16, sight; 17, hearing; 18, taste; 19, joint movements of head and eye; 20, hip-joint; 21, knee; 22, ankle; 23, great toe; 24, smaller toes.

trunk (1) are innervated from the part of the marginal gyrus in front of the paracentral lobule.

The involuntary muscles stand, in all probability, in no direct dependence on the cortex of the brain.

With regard to the voluntary muscles, it may be laid down as a law that the more completely subject any muscle-group (or limb) is to the will, the more largely is it represented in the cortex of the brain; and, on the other hand, the more a muscle group acts without the intervention of consciousness (that is to say, reflexively), the slighter is its connection with the cortex and the smaller the space allotted to it therein.

The functions of a large part of the parietal lobe have not yet been cleared up (centre of the muscular sense?).

The occipital lobe, its cuneus certainly, and the neighbouring portion of the parietal lobe (that is to say, the gyrus angularis, *Ferrier*), are connected with the sense of sight (16). This region is the seat of sight-perceptions for the temporal half of the retina of the same side, and the nasal half of



the retina of the opposite side. The motor centres for the extrinsic eye-muscles probably lie in the anterior part of the inferior parietal lobule (according to *Mott* and others, in the lower part of the frontal lobe).

The temporal lobe certainly stands in the same relation to perceptions of sound (17), as the occipital lobe to perceptions of sight; this holds good for the upper convolution and the gyri temporales transversi, which take rise from it only (*Flehsig*), or at the most for this and the middle convolution. The anterior part of the temporo-sphenoidal lobe, especially the region of the uncus and the cornu Ammonis, is intimately connected with the olfactory apparatus, and possibly also with the organs of taste. All the rest of this very important region is, in its physiological relations, as yet unexplained.

The localisation of cutaneous sensibility in the cortex of the brain is as yet very imperfectly understood. A view often advanced is that the regions which supply nerves to certain muscles act also as centres of cutaneous sensibility to the corresponding parts. This is not borne out, so far, by clinical observation; for in many cases of crossed paralysis of the cortex the cutaneous sensibility is not affected in any marked degree. *Brissaud* would account for this circumstance by supposing each hemisphere to receive tactile impressions from either side. According to his explanation the sensory tract divides in the centrum semiovale, one part proceeding to the cortex on the same side, and the other passing through the splenium corporis callosi to the corresponding region of the farther hemisphere. *Charcot* and *Pitres* regard the disturbances of sensibility which, in about a third of the cases, accompany cortical paralysis, as purely functional, the condition being analogous to hysterical anæsthesia.

*Horsley* and *Schäfer* are of opinion that the gyrus fornicatus stands in some relation to sensations of touch and of pain. This would oblige us to assume that the various forms of cutaneous sensibility, such as the feeling of warmth, are connected with special local centres, a view to which clinical experience lends no support whatever.

A number of complicated special functions of the cortex appear to be associated with particular regions, especially those connected with the faculty of speech. Thus, motor aphasia (10) is the outward sign of a disease of the posterior part of the gyrus frontalis on the left side (Broca's convolution). Agraphia (8) has been attributed, though with less justification, to the posterior part of the gyrus centralis, and word-blindness (the darker portion of 16) to the gyrus angularis.

It must always be borne in mind that a sharp delimitation of the cortical centres does not in effect exist, and that such localisation can only be attempted with regard to motor and sensory processes, and cannot possibly be applied to those which are purely psychical. Probably individual variations are present in no slight degree. As far as is known the portions of the cortex hidden away in the fissures join in function with the superficial parts.

With regard to the fissures, it is not yet decided whether they simply serve the purpose of increasing the superficial spread of the cortex, or also



at the same time serve to mark out territories physiologically distinct. [No question in the comparative anatomy of the brain concerns the neurologist more closely than the question as to the morphological value of the fissures. Are they merely plaitings of a shifting surface, or are they definitely fixed in their topographical relations to the several organs which the cortex comprises? A study of the development of the fissures in the brains of animals which stand far apart in phylogeny teaches that they appear with such regularity as to sequence and progressive extension, and obey such definite rules as to relative depth as would, in the case of other parts of the body, justify us in considering them as of organic significance. The so-called fissure of Sylvius is a boundary between organs of different functions; but a true fissure, such as the Rolandic or the calcarine fissure, is more probably a centre of functional concentration.] According to the views above set forth the second object could, owing to the partial overlapping of the centres, be effected to a limited extent only by the fissures.

This much may be taken as certain—the fissuring of the cortex of the great brain effects an increase in its superficial area. The same holds good for the cerebellar cortex, and in the deeper parts for the convolutions of the inferior olive and the corpus dentatum cerebelli. Plaits of the vascular pia mater extend into the fissures of the cerebrum and cerebellum, carrying thus to its substance the greatest amount of nutriment possible. From this point of view the fissures are nutrient in function (*J. Seitz*).

For all convolutions the law holds good that the thinner the cortex the narrower the convolutions. Hence the occipital convolutions are the narrowest of those of the great brain. The cerebellar convolutions are still narrower.

There can be no manner of doubt that skull-case and skull-contents mutually influence one another's growth, but it would be quite a mistake to trace the arrangement of the convolutions to the resistance offered by the wall of the skull.

The several regions of the surface of the brain (and not they alone, but also its inner parts and vessels) have been proved to stand topographically in an invariable relation to the bones of the skull. Consequently, we are able to point out in the exterior of the skull the spot beneath which any given part of a convolution is situate. This very exact knowledge of the topography of cranium and brain enables us to treat many cases of localised brain disease successfully by operation, provided the seat of the disease is indicated by the symptoms. But in order to make sure of the course of convolutions and fissures in the living subject, we must first take certain fixed and easily recognisable points (points de repères), and, proceeding from these, determine by measurement and calculation the exact spot we are in search of. It is obvious that these 'points de repères' ought to be such easily discoverable land-marks as the meatus auditorius externus or the inion (protuberantia occipitalis externa). To give the preference to the sutures of the skull is a great mistake from this point of view, as only



in very rare cases can they be felt distinctly through the scalp. A detailed discussion in this place of the relation of the surface of the skull to the cerebral convolutions would lead us too far. The subject is fully treated in many text-books, *e.g.*, Chipault's *Chirurgie Opératoire*.

From the study of the exterior conformation of the cerebrum we have already gained some knowledge of the **development of the fissures**.

We have seen that the first to be formed is the fossa Sylvii. In the third and fourth months a few furrows appear, tending towards the fossa Sylvii. These disappear by the fifth month, and must therefore be regarded as transient primary fissures. Of the permanent primary (or total) fissures the arcuate (*sillon ammonique*, sulcus corporis callosi, together with fissura hippocampi) appears in the embryo in the second month, the calcarine and parieto-occipital fissures in the fourth.

The secondary fissures develop during or after the sixth month, the most important being also the first to appear (sulcus centralis, præcentralis, interparietalis, calloso-marginalis). Other furrows are added in increasing numbers, so that at the time of birth the distribution of fissures and convolutions is almost complete. According to *Sernoff* both fissures and convolutions have attained their final form in the fifth week of post-embryonic life.

In a **comparison of the convolutions of the brain** in animals only the brains of mammals can be taken into account, as the cerebrum of the remaining classes exhibits no convolutions whatever. Even among the

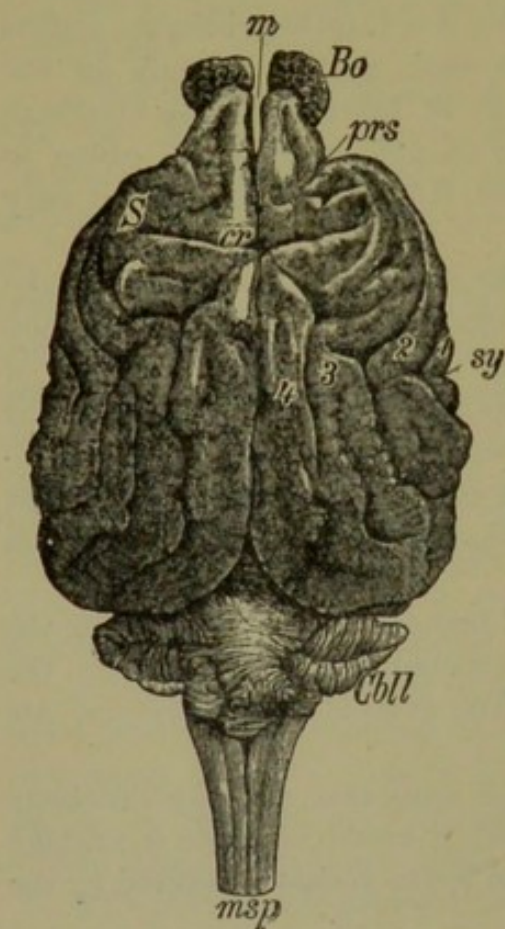


Fig. 35.—Brain of dog as seen from above (*natural size*).—1, 2, 3, 4, the four arched convolutions; Bo, bulbus olfactorius; Cbl, cerebellum; cr, sulcus cruciatus; m, longitudinal fissure; msp, medulla spinalis; prs, sulcus præ Sylvii; S, gyrus sigmoides; sy, Sylvian fissure.

mammalia we find some small animals in which the brain presents a smooth or almost smooth surface. *Owen* has given the name of 'lissencephalous' mammals to these, as distinct from the 'gyrencephalous,' or those in which the brain exhibits fissures and convolutions. Within the mammalian order the more complex brain pertains, as a rule, to the larger animals, but the richness in fissures, like other factors, depends both on the size of the animal and also on its intelligence (*Krueg*). There are still



very great difficulties in the way of a sound classification based on the relations of the convolutions to one another.

Starting from the Sylvian fissure, we observe that in most animals the main fissures assume the form of an arch, more or less sharply curved, with its axis oblique to the Sylvian fissure. (This formation is especially well-defined in beasts of prey.) Hence it has been concluded that this is the original type of convolution (*Huschke*). Against this it may be advanced that the brains of the primates and of Man bear only a somewhat remote resemblance to this supposed original type.

In beasts of prey we observe three or four arcuate fissures defining the convolutions (sometimes three in number, as in *Lutra* and *Mustela*; sometimes four, as in *Canis* and *Felis*) which curve round the Sylvian fissure (fig. 35, 1, 2, 3, 4). We further observe, in the anterior part of the brain, two other fissures deserving of special mention, as both characteristic and physiologically important.

One, rising on the margin of the mantle, traverses the convex surface of the hemisphere laterally for some distance. The corresponding fissures of the two hemispheres meet at right angles to the longitudinal fissure, forming a cross, to which it owes its name, sulcus cruciatus (fig. 35, *cr*). The name of gyrus sigmoideus (fig. 35, *S*) has been given to the convolution which passes round this fissure from the end of the uppermost of the arches. The second of these noticeable fissures, sulcus præsylvius (fig. 35, *prs*), passes diagonally upwards and forwards from the fissure which bounds the hemisphere towards the lobus olfactorius. In the figure representing a dog's brain viewed from above, the anterior and upper end of this fissure is visible in front of the gyrus sigmoideus.

In the brain of cetaceans, which is peculiarly rich in fissures, the same arrangement of four arcuate convolutions may be traced, though complicated by numerous small irregularities.

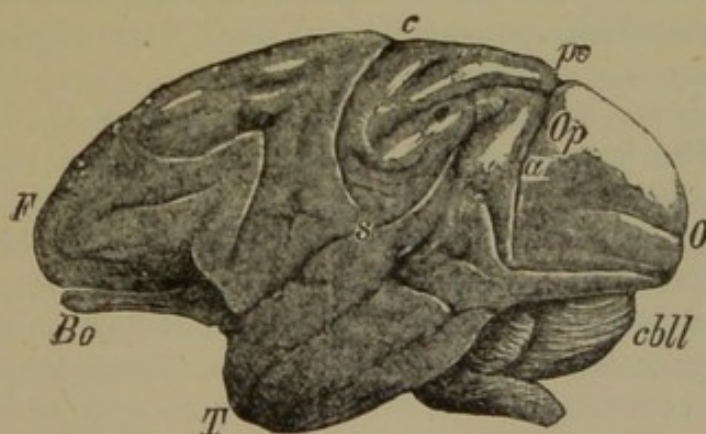


Fig. 36.—Brain of *Cercopithecus* (natural size).—*a* (Affenspalte); *Bo*, bulbus olfactorius; *c*, central fissure; *cbll*, cerebellum; *F*, frontal pole; *O*, occipital pole; *Op*, operculum; *po*, parieto-occipital fissure; *s*, Sylvian fissure; *T*, temporal pole.

In the apes we are confronted with a singular state of things. While the brains of the smallest (*Hapale*) exhibit an almost unfurrowed surface, the first thing we notice in those of the larger forms (*Cercopithecus*,



Cynocephalus, and others) is a fissure which can be identified without difficulty as the sulcus centralis (fig. 36, *c*). But the striking peculiarity of all, except in the anthropoid apes, is another deeply-cut fissure, the Affenspalte (fig. 36, *a*), which defines the anterior boundary of the occipital lobe,—in itself nearly destitute of convolutions. Near the margin of the mantle it passes over into the fissura parieto-occipitalis, and so might easily be taken for the lateral part of that fissure very strongly developed. As a matter of fact, however, it owes its existence to the bulging forward of the occipital lobe, which forms an easily lifted operculum over the deeper parts of the parietal lobe (the gyri annectantes of *Gratiolet*).

In the frontal lobe, as represented in fig. 36, we see at the top the short sulcus frontalis superior; below it is the remarkably acute angle of the sulcus arcuatus; lower still the sulcus rectus, and on the margin of the orbital surface the sulcus orbitalis lateralis.

The brains of anthropoid apes approximate in many respects to the human type.

**Size and Weight of the Brain.**—The utmost that we can expect to gain from an investigation of the size of the brain is some light upon its **capability** of intellectual functions. The development of this rudimentary capability depends on various outward circumstances, many of them merely social; and to trace the effect of these is beyond the scope of even the minutest investigation. From this it follows naturally that we shall look in vain for any exact agreement between intellectual capacity and the size of the brain.

But there is another and far more important condition which deranges a correspondence we might naturally be disposed to take for granted. Of two brains of equal size, one may be capable of producing work of a much higher order than the other, in consequence of the greater accuracy and nicer adjustment of the interior structure, the more delicate construction of the elements which compose it, and their finer adaptation to their several functions.

Usually, it is not the actual size but the weight of the brain which is determined. The first point to investigate is, therefore, the relation of brain-weight to intellectual capacity.

Before weighing the brain the inner membranes should be removed. According to *Broca* the average weight of these membranes, including the serum contained in the subarachnoidal spaces, is 55·8 grms. in the brains of men and 48·7 grms. in those of women. *Morselli* found the average much higher in cases of mental disease, even apart from such as involved great changes in the meninges. He places it at 124·5 grms. and 93·3 grms.

Again, there is no hard and fast line between brain and spinal cord; opinions differ slightly as to the proper place for dividing them; nor, indeed, is it always possible to hit upon exactly the same spot. This makes a difference of several grammes. Finally, a variable amount of the fluid contained in the brain cavities flows out, causing a perceptible difference in the total weight.



Confining our observations to the adult brain, we find that its weight averages 1360 grms. in men and 1230 in women.

Causes other than sex, which should be noted as exercising some influence on the weight of the brain, are: age, height and weight of the body, race, and, finally, certain morbid conditions which induce an increase or decrease of brain-weight.

With regard to age, it has been proved that the brain grows rapidly in early life, and reaches the maximum point of its development at about twenty years of age. It then remains stationary up to sixty in men and fifty in women. From that period onward we note a steady decrease.

By 'relative brain-weight' is meant the ratio of the weight of the brain to that of the whole body. *Thurnam* estimates it at 1 to 33 in men and 1 to 31.9 in women. But according to *Mies* the ratio in new-born children is 1 to 5.9. The brain is therefore relatively much heavier at birth than in mature life. It must not be forgotten that relative brain-weight varies greatly according as the subject is well or ill nourished. *Thurnam's* figures can only be accepted as applying to very debilitated persons; in the healthy we may certainly assume the ratio to be not lower than 1 to 50 or 1 to 60.

A comparison of the brain-weight of different adults with reference to the height of the body shows that the increase of the former does not keep pace with that of the latter. For example, in men 150 centimeters in height we find the ratio to be 8.7 grms. of brain to every centimeter, while in men 190 centimeters in height it is only 7.1 grms. to the centimeter. At birth the ratio is 1 gm. to 1.35 millimeter in boys, and 1 gm. to every 1.41 millimeter in girls.

With regard to racial differences the data before us at present are wholly insufficient, and no inferences drawn from them can pretend to be conclusive.

When the brain itself cannot be put on the scales we may gain a tolerably accurate idea of its size by measuring the hollow of the skull; though I need hardly say that calculations of this sort stand in need of correction in some respects. They enable us, however, to estimate the brain-weight of races known to us only by skulls in anthropological museums, and even of races now extinct. *Broca* examined 115 twelfth-century skulls by this method and found that their capacity averaged 1426 cubic centimeters, while the average capacity of 125 nineteenth-century skulls (of Parisians only) was 1461.5 cubic centimeters,—that is to say, considerably greater. From this he infers a corresponding increase of brain-weight.

Few animals possess a brain heavier than that of Man.

The heaviest brain is that of the whale, the brain of *Balænoptera Sibbaldi* occasionally attaining, according to *Guldberg*, the weight of 6700 grms. and more. The brain of the elephant sometimes weighs as much as 4000 or 5000 grms. (according to *Crisp*, 5430 grms.). In the horse, on the other hand, it weighs only from 600 to 680 grms., and in the ox from 400 to 500. The brain-weight of the gorilla never exceeds 500 grms.



Relative brain-weight differs much more widely in animals than in Man. It is not the fact that Man possesses relatively the heaviest brain; some singing-birds and small apes surpass him in this particular.

Any attempt to discover a parallelism between intellectual capacity and brain-size, as determined by weight, leads us to the conclusion that such parallels can only be admitted with the greatest reserve.

The comparison of a large number of brains undoubtedly shows that, as a matter of fact, the proportion of heavy brains is larger among men engaged in intellectual pursuits, and that, on the other hand, light brains are in the majority among the lower uneducated classes; but in individual cases we are as little justified in regarding a heavy brain as a sign of pre-eminent ability as in supposing that a light brain (so long as it does not fall below a certain weight) must necessarily go with intellectual inferiority. The brain-weight of the great statesman Gambetta was only 1100 grms. [1241 grms., see p. 110], while, on the other hand, there are three cases on record in which the brain weighed more than 2000. One of the three was that of a working man of the name of Rustan (*Rudolfi* gives its weight as 2222 grms., but later calculations set it at barely over 2000); another, that of the great writer Turgenieff (2012); and the third, that of a man of good social position and moderate abilities (about 2028). In one case *Lorey* found that the brain of a boy of six years old weighed 1840 grms.

The minimum weight, short of which the brain cannot fall without a marked enfeeblement of the mental faculties (idiocy), may be fixed at 1000 grms. for men and 900 for women. In the case of a woman who died in an asylum at Vienna the brain was found to weigh 740 grms., which is exceptionally light for a half-witted person (*Hess*). In idiots the brain-weight sometimes falls below 300 grms.; the lightest on record is mentioned by *Marshall* as weighing 241 grms. That of the idiot Mottey weighed 369 grms.

We can, therefore, safely assert that a relation between brain-weight and intelligence can only be said to exist in so far as (generally speaking) the heavier brains are found among the more highly civilised races and the classes engaged in intellectual pursuits; and, also, that to insure the normal exercise of the psychical functions the brain must exceed a certain minimum weight.

On the ground that in judging of intellectual capacity the cortex alone should be taken into consideration, attempts have been made to ascertain the superficial area of the brain by direct measurement. But since for this it is necessary to penetrate to the bottom of all the fissures which bound the convolutions, the problem presented by the human brain is a hard one to solve. Of all methods as yet practised, that of *Hermann Wagner*, tedious as it is, has yielded the most accurate results. The whole surface of the brain is covered with small pieces of gold-leaf, which are afterwards put together (or, in some cases, weighed), the total thus representing the entire superficial area. In the brain of Gauss, the mathematician, this total amounted to 221,005 square millimeters, or an area



equal to a square not quite half a meter long. *Wagner* estimated the total superficial area of a working man's brain at no more than 187,672.

An exact knowledge of the weight of the several parts of the brain would be of great value; but as the division is necessarily more or less arbitrary, the figures obtained by weighing them separately must be accepted with caution. *Meynert's* very careful experiments have given the following ratio for cortex, brain-stem, and cerebellum:—

	Cortex.	Brain-stem.	Cerebellum.
In men, . . .	78·5	11·0	10·5
In women, . . .	78·3	11·1	10·6

He found that the weight of the cortex varied from 1250 grms. to 570 grms., of the brain-stem from 168 to 84, and of the cerebellum from 180 to 99.

It must not, however, be forgotten that *Meynert's* calculations were made only from the brains of adult lunatics.

The two hemispheres are nearly alike in weight, though *Boyd* and others have found that the left is almost always the heavier by a few grammes. The right is said to be the heavier in left-handed persons (*Ogle*), and *Lombroso* maintains that it is so in criminals.

The element of uncertainty inseparable from the method of weighing in parts is most strongly felt in dealing with the cerebrum, as we have hardly any definite lines of demarcation to guide us in subdividing it into lobes. [For reasons already stated (p. 99) great errors may be made by accepting the fissures as delimiting lines.]

From *Meynert's* calculations we see that in the insane the lightest weight is associated with dementia paralytica or chronic alcoholism. In paralytic imbecility the shrinkage affects the cortex almost exclusively, the cerebellum suffering hardly any diminution. As I have mentioned before, the lightest brains of all are found in idiots, among whom the brain-weight touches its minimum. Inequalities of weight in the two hemispheres are commoner in insane persons, and occasionally more considerable. Any difference that exceeds 20 grms. must certainly be regarded as abnormal.

From experiments in weighing a large number of brains *Pfleger* comes to the conclusion that in persons who have died of chronic disease the brain loses from two to five per cent. of its original weight, and that the loss affects its three main divisions almost equally.

The average weight of the spinal cord is about 28 grms.

The specific gravity of the brain *in toto* cannot be estimated with certainty by our present methods; but, on the other hand, *Sankey's* method is admirable for determining the specific gravity of small pieces, and dispenses with the need of minute accuracy in the scales. Solutions of salts (sulphate of magnesia is the best) should be made of varying strengths, from 1·026, 1·028, etc., up to about 1·059, making fourteen solutions in all. A very small piece of the part of the brain to be examined should then be placed in one of the solutions. If it sinks, its specific gravity is higher than that of the fluid; if it stays on the top, it is



less. When it floats in the fluid the proper degree of concentration has been found. If, however, it sinks in 1·034 and floats on 1·036 its specific gravity lies between the two at 1·035. The piece of tissue should be observed at the moment of immersion, and the formation of adhering air-bubbles should be guarded against.

The subjoined table gives the average specific gravity of the several parts of the brain as computed from a large number of cases.

CEREBRUM.											CEREBELLUM.					
Left Hemisphere.				Right Hemisphere.												
Cortex.																
F.	P.	O.	T.	F.	P.	O.	T.	Medulla.	C. str.	Th. opt.						
1·0308	1·0325	1·0360	1·0330	1·0308	1·0325	1·0362	1·0326	1·0412	1·0378	1·0402	1·0376	1·0412	1·0400	1·0413	1·0371	

The cortex is invariably lightest in the frontal lobe, and heaviest in the occipital, the cortex of the temporal and parietal lobes standing halfway between. The central medulla has the same specific gravity in the cerebrum and the cerebellum; the pons is a trifle heavier.

The specific gravity of the thalamus opticus is higher than that of the corpus striatum; in fact, a greater richness in medulla always causes a rise in specific gravity. If the thick cortex of an anterior frontal convolution be divided into three equal layers their specific gravity from without inwards will be found to be 1·028, 1·034, 1·036.

The innermost layer, permeated with the coarse radial fibres, is thus seen to be the heaviest. In the middle layer the radial fibres are still abundant, while it is evident that in the outermost layer the tangential fibres are too thinly spread to compensate for the lack of radial fibres.

To obtain an accurate idea of the effect of various circumstances, such as age, sickness, etc., on the specific gravity of the brain and its component parts, a very lengthy series of observations would be necessary. As the specific gravity of the blood, however, is higher than that of the brain (1·055), we may assume that a hyperæmic brain will have a higher specific gravity than an anæmic one.

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### SECTION III.—HISTOLOGICAL ELEMENTS OF THE CENTRAL NERVOUS SYSTEM.

FOR a right apprehension of the structure of the central nervous system a knowledge of all the elements of which it is composed is absolutely necessary.

It is not exclusively composed of nervous elements; indeed these are enfolded in a network of other structures which serve for their nutrition and support.

The investigations of the last few years have profoundly modified our conception of the value of the histological elements of the nervous system. Conflicting opinions are still held on many points of primary importance, which can only be decided by further investigation.

The following is a summary of all the different kinds of tissue met with in the central nervous system, of each of which we shall have later on to give a detailed account:—

#### A. Tissue ectodermal in origin.

1. Nervous constituents: (a.) Nerve-fibres.  
(b.) Nerve-cells.
2. Non-nervous constituents: (a.) Epithelia.  
(b.) Neurogleia.

#### B. Tissue mesodermal in origin.

1. Connective tissue.
2. Vessels.

### A. TISSUES OF ECTODERMAL ORIGIN.

#### I. NERVOUS CONSTITUENTS.

The two main constituents which come under this head are treated separately for the sake of convenience only. As a matter of fact, each nerve-fibre with its appertaining cell forms a separate histological unit. The results of the most recent investigation constrain us to regard each cell, together with the fibre that starts from it, as a histological entity, a nerve unit, which has been variously named neuron (*Waldayer*), neurodendron (*Kölliker*), or neuria (*Rauber*). (Fig. 37.)



The accompanying diagram shows a nerve-cell, (I.) from which a nerve-fibre (II.) takes rise, starting from a process, *a* (the axis-cylinder process). The fibre ramifies at the farther end, splitting up finally into a number of fine branches which compose the arborescent system, III. We further see a number of other much-ramified processes, *p* (the protoplasmic processes),

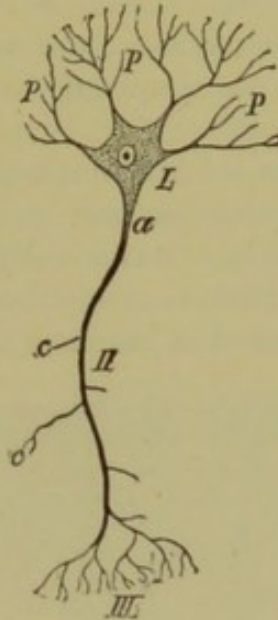


Fig. 37.—Diagram of a nerve-unit (neuron).—I., the nerve-cell; *p*, protoplasmic processes; *a*, axis-cylinder process; II., nerve-fibre with collaterals (*c*); III., arborescent system.

in connection with the cell, and side-branches, *c* (the collaterals) given off from the nerve-fibre. The combination of all these parts forms a neuron, which is, histogenetically, a unit.

The relations of the neurons to one another and to the other tissues must be treated of later.

#### (a.) NERVE-FIBRES.

We shall soon see that we must distinguish several kinds of nerve-fibre; there is, however, one histological constituent, **the axis-cylinder**, common to them all, for its presence is characteristic of a nerve-fibre. The axis-cylinder can only with difficulty be seen in fresh peripheral nerve-fibres. It is only distinct after the action of various reagents; so that for a time people doubted its existence in the living fibre, and took it to be an artificial product.

There are various methods for bringing out the axis-cylinder. A fresh nerve should be taken from a recently killed animal—for example, the sciatic nerve of a frog serves particularly well on account of its large fibres; a part is finely teased as quickly as may be without the addition of anything except a little serum, placed on a slide, care being taken that the individual fibres are long and spread straight out. Afterwards collodion is put round the preparation, and it is covered with a cover-slip. The axis-cylinders are then seen as darker bands traversing the centre of



the fibres; such a preparation can only be kept a short time. Or the nerve-fibres may be teased in *Ranvier's*  $\frac{1}{3}$  alcohol (two parts of water to one of 90 per cent. alcohol).

If a coarsely-teased piece of fresh nerve is laid for twenty-four hours in a weak solution of perosmic acid (0.1 per cent.), and then, after washing, more finely teased, a preparation is made which shows the axis-cylinder as a central clear band, as well as various other details of structure presently to be described. Such fibres can afterwards be coloured with picrocarmine, fuchsin, and other reagents.

In preparations of sections cut from a spinal cord or medulla oblongata hardened in bichromate of potassium and stained in carmine, the nerve-fibres show either longitudinally or transversely, according to the plane of the section, with the axis-cylinders clearly defined in red (fig. 38). Peripheral nerve-stems can be treated in the same way or teased.

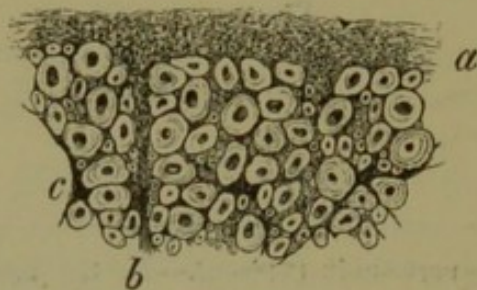


Fig. 38.—Cross-section from the anterior columns of the spinal cord, stained in carmine. *Magn.* 150 diam.—*a*, Peripheral grey cortex layer; *b*, smaller septum. In the medullary substance, besides the cross-sections of larger and smaller medullated fibres, three distinct stellate connective-tissue cells are seen; one of these is indicated by the letter *c*.

By these methods the axis-cylinder appears as an almost homogeneous band, which presents numerous curves and irregularities due to the methods employed for hardening. *Fleischl* says that the axis-cylinder is better preserved in fibres hardened in alcohol.

By employing other reagents, further details in the structure of the axis-cylinder may be brought to light. It can be resolved into a hollow membrane 'axis-cylinder-sheath' filled with stiff protoplasm, or, according to others, with fluid protoplasm, in which a number of exceedingly fine fibres are included (primitive fibrillæ). The number of these fibrillæ depends upon the thickness of the axis-cylinder. *Kupffer* counted over a hundred in the thicker fibres of the frog's sciatic nerve; their diameter (which varies very considerably) is nearly always so inconsiderable that it is impossible to measure them, even when very highly magnified. In the centre of the axis-cylinder these fibrillæ are mostly closely packed, while the peripheral part often appears destitute of fibrillæ. The large nerve-fibres in the abdominal cord of the crayfish, examined in a drop of the animal's blood, show these bundles of fibrillæ as a central fasciculus (*Remak, Freud*). After maceration of fresh nerve-fibres in weak chromic acid, the fibrillar structure of the axis-cylinder becomes sometimes distinctly visible. For permanent preparations *Kupffer* recommends the following method. The



nerve is fixed in a condition of physiological extension, which can be accomplished (as suggested by *Ranvier*) in the following manner:—The nerve is fastened by means of a ligature at either end to a little rod of wood (*e.g.*, a match) which has previously been cut thin at the middle. Nerve and wood are then laid for two hours in a 0·5 per cent. osmic acid solution, washed for two hours in distilled water, and then placed from one to two days in a strong watery solution of acid fuchsin. *Jacobi* finds that a concentrated solution of Bismarck-brown used in the same way yields better results. After that, it is washed for six to twelve hours in absolute alcohol, cleared in clove-oil, embedded in paraffin (maintained for twenty-four hours just above its melting-point), and after that cut in longitudinal and cross-sections. Such preparations show the primitive fibrillæ in an otherwise uncoloured axis-cylinder. At those particular spots in the nerve, which we shall know later on as *Ranvier's nodes*, the individual fibrillæ come close together (*Boveri*). The theory of the existence of primitive fibrillæ has been maintained with remarkable acumen of late by *Apáthy*. I shall return to the consideration of this point, as well as to *Held's* view, at a later stage. Several other modern observers see a fine network, a kind of connective tissue, extending through the whole axis-cylinder. According to one view (*M. Joseph*), the course of the fibrillæ lies through this tissue; according to another, there are no fibrillæ at all, and the connective tissue itself is to be regarded as a contractile substance (*Heitzmann*).

*Leydig* and *Nansen* (with whom *Retzius* in some measure agrees) give a totally different account of the structure of the axis-cylinder. They look upon it as made of a large number of closely packed 'primitive tubes'; these cylindrical tubes consist of an extremely fine connective-tissue sheath (spongioplasm) and viscous contents (hyaloplasm). According to this view, the 'primitive fibrillæ' are an illusory appearance produced by the thickened parts of the spongioplasm; and the constituent of highest physiological importance in the axis-cylinder is to be sought, not in these supposed fibrillæ, but in the fluid, which was formerly thought to serve for filling the interstices between them.

If small pieces of the spinal cord of a recently-killed animal are left for eight to fourteen days in a weak solution of silver nitrate (1 in 400) in the dark, washed in water, and then, after teasing, exposed for a short time to daylight in a drop of glycerin and distilled water, many axis-cylinders are



Fig. 39. — Medullated peripheral fibre. Hardened in potassic bichromate, stained in carmine; teased. Magn. 200.—*a*, Axis-cylinder; *b*, *Ranvier's node*; *c*, nucleus of Schwann's sheath.



met with amongst its fibres, which for some part of their course appear coloured brown by the silver, owing to their being divested of their medullary sheath. On close observation it is seen that this coloration is not continuous for the most part, but made up of a succession of darker and lighter cross-bands. The width of these bands varies from 1 to 4  $\mu$ ; on any small piece of the axis-cylinder, it is, however, regular, the cross stripes being in strong contrast with the longitudinal striation which the former methods have shown us.

This brown coloration with silver nitrate looks as if it affected the axis-cylinder itself; as a matter of fact, however, it colours a delicate membrane investing the tube in which the axis-cylinder substance, with its primitive

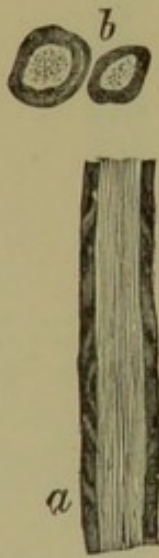


Fig. 40.—Peripheral nerve-fibres of the frog. *Perosmic acid and Bismarck-brown*. Magn. 1000.—*a*, Longitudinal section; *b*, cross-section.



Fig. 41.—Axis-cylinder of a fibre from the white substance of the spinal cord. Its sheath stained with silver nitrate exhibits Frommann's stripes. At *a* the axis-cylinder is naked. Magn. 400.



Fig. 42.—A fresh medullated nerve-fibre from the sciatic of the frog. Magn. 200. Commencing coagulation of the myelin.—*a*, The axis-cylinder projecting free; *b*, escaping drops of myelin.

fibrillæ, is contained—**axis-cylinder sheath**. Often one sees the uncoloured coagulated axis-cylinder projecting for some distance out of its brown sheath. A striation, which marks the silver-stained sheath, first described by *Frommann*—hence known as *Frommann's cross bands*—is found not only in peripheral nerves, but also in the not yet medullated fibres of the spinal cord of new-born animals. As it is also found in the adventitia of the vessels and other non-nervous tissues, it cannot be regarded as in any sense characteristic of the axis-cylinder (*Rabl, A. Fischel*). The phenomenon belongs to the province of physics rather than to that of histology. The axis-cylinder-sheath is in most nerve-fibres surrounded by still other investments, by the medullary sheath, Schwann's sheath, and the



fibrillar sheath [Henle's sheath]. These three sheaths are found in most peripheral nerves, and hence may next afford us material for observation.

The **medullary sheath** which surrounds the axis-cylinder-sheath soon begins to coagulate, especially its outer layers, in freshly prepared nerves, producing the appearance characteristic of doubly-contoured nerves (fig. 42). Later on the medulla coagulates right up to the axis-cylinder in globular masses, which greatly alter the appearance of the fibre. *Boll* has made a very minute study of this condition. At the cut ends of the nerves, these coagulation-products escape from the sheath of Schwann as peculiar rounded drops of various shape with a double outline.

With *Gad* and *Heymanns* we may assume that this myelin-formation is due to maceration-products in the lecithin present in the medullary sheath, attended by the formation of membranes in the precipitate.

The greater number of stains, such as carmine, for example, are absorbed but little by the medullary sheath, so that, in most methods of staining, this sheath is left nearly or quite uncoloured. A transverse section of a peripheral nerve, or of the white columns of the spinal cord, shows colourless rings of medulla, usually stratified concentrically, surrounding coloured axis-cylinders. Sometimes some of these rings are stained (fig. 38) in such a way that either the cross-sections of certain nerves are coloured while others remain untouched; or certain nerves show several concentric rings of colour. This really depends, however, upon the coagulation-process, and not upon any histological differences which might have physiological bearings. In longitudinal sections many nerve-fibres appear irregularly tinted, since for a distance the medulla is colourless and then again coloured. Only the outer peripheral part of the myelin sheath is doubly-refracting (*Bechterew*, *Diomedow*). If this is really the case we must infer from it a radical difference in structure between the outer, or peripheral, and the inner, or periaxial, layers of the medullary sheath. The object of several methods, as, for instance, Weigert's hæmatoxylin method, is to colour the medullary sheath.

Nerve-fibres which have been placed for twenty-four hours in a weak solution of perosmic acid (0.1 to 0.2 per cent.), examined in glycerin, show that the medullary sheath is not continuous. It is best to maintain them during this immersion in a condition of physiological extension. The medullary sheath is broken at regular intervals (1 to 2 mm. apart in the frog), leaving a space between the segments. The myelin sheath is somewhat enlarged as it approaches the interruption, at either side of which it ends while the axis-cylinder extends across (fig. 45). These gaps were first described by *Ranvier*, and hence are known as *Ranvier's nodes* (*étranglements annulaires*). They are to be seen, although less clearly than in specimens prepared as above, not only in freshly-prepared nerves, but also in the living nerve in the frog's lungs (*Rawitz*). This proves that they are not artificial products.

These nodes break up the fibre (all but the axis-cylinder) into a chain of segments, to which *Ranvier* gave the name of 'segments inter-annulaires.' They are not of uniform length, being as a rule shorter in the thinner



nerves and towards the peripheral end of the fibre. *Ranvier* estimates their average length in Man at about 1.1 mm.

The nitrate of silver method is of great service in the study of these nodes.

A thin fresh nerve-fasciculus is washed in water and then placed in a solution of nitrate of silver (3 in 1000) for from ten minutes to an hour at most. It is again washed in water, and then examined in glycerin. The glycerin should replace the water only by slow degrees. After exposure for a short time to light of ordinary strength, such a nerve-bundle shows, under a low power, numbers of black crosses occurring at intervals (fig. 44). The meaning of these crosses is not made out until after teasing the fasciculus with needles. Now it is seen that each cross consists of a vertical and a horizontal bar; the latter extends from the periphery to the sheath of the axis-cylinder, and corresponds to a silver-impregnated diaphragm which occupies the situation of *Ranvier's* node, separating the two ends of the medullary sheath. It may therefore be called the intermedullary sheath. Through its central aperture passes the axis-cylinder. *Ranvier* called this diaphragm the 'biconical swelling,' because the middle part, which closely invests the axis-cylinder, is usually the thickest. In preparations the peripheral part of the diaphragm, being thinnest, is apt to tear and to be thrust more or less away from the situation of the node by the displacement of the axis-cylinder within the medullary sheath. The vertical bar of the cross depends upon the impregnation with silver of the ends of the axis-cylinder sheath. The farther from the intermedullary sheath the fainter becomes the transverse staining of the axis-cylinder. The intermedullary sheath, which is unstained by osmic acid, constitutes a connection between *Schwann's* sheath and the axis-cylinder sheath.

In osmic preparations it is further seen that the medullary sheath is formed of segments which, arranged like overlapping funnels, surround the axis-cylinder. Such a segmentation was known to *Stilling*, and was again described, simultaneously, by *Schmidt*, *Lantermann*, and *Zawerthal*. These medullary segments may be products of the method; but under any circumstances their regular arrangement depends upon some pre-existing quality in the medulla which demands our attention.

**Schwann's sheath** (*membrana limitans*, external neurilemma) is a thin, delicate, but yet firm membrane, which closely invests the medulla; hence it is, as a rule, no more visible than the axis-cylinder sheath. *Schwann's* sheath is exhibited when, by slight pressure on the glass covering freshly-isolated peripheral nerves, some of the medulla is squeezed out from the tubes which contain it.

*Golgi*, *Rezzonico*, and others, have detected in *Lantermann's* constrictions peculiar spirally-arranged fibres, to which they ascribed the function of supporting the medulla. It seems probable that these fibre-cones have no pre-existence in the living nerve.

*Ewald* and *Kühne* base on their digestion-method (with pepsin and trypsin) the opinion that the whole myelin sheath is traversed by a close-set network of horny substance (*neuro-keratin*). *Stilling* had long ago so



represented the constitution of the fibres. This horny substance does not, however, appear to exist in the living nerve. For rendering visible the network in the myelin sheath the method recommended by *Platner* is a good one. Thin fresh nerve-stems are placed for several days in a mixture of 1 part liquor ferri sesquichloridi and 4 of water; then well washed, and transferred to a concentrated solution of dinitrosoresorcin (German Pharma-



Fig. 43.—Nerve-fibre from the sciatic of the frog, after treatment with osmic acid. *Magn.* 400.—*a*, Ranvier's node; *b*, nucleus of Schwann's sheath. The darkly-stained medullary sheath exhibits the clefts which separate *Lantermann's* cones.

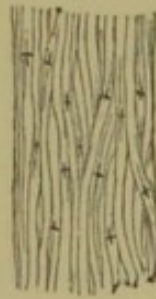


Fig. 44.—A short piece of a thin peripheral nerve treated with nitrate of silver. *Magn.* 30. It shows numerous nodes of *Ranvier*.

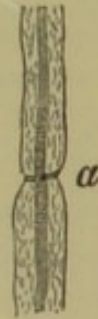


Fig. 45.—An isolated medullated fibre treated with silver nitrate. *Magn.* 200.—*a*, a *Ranvier's* node.

copœia) in 75 per cent. alcohol. After some days the pieces will be stained dark-green throughout. They can then be teased, or embedded for cutting into thin sections. *Lantermann* also saw and represented a fine network (*Lantermann's* net) in the medullary sheath, but this must not be identified with the neuro-keratin framework of *Ewald* and *Kühne*, as it becomes intensely black when exposed to osmic acid.

*Paladino* goes so far as to think that the whole myelin sheath is permeated with fine fibrillæ connected with the neurogleia cells.

Between each two nodes of *Ranvier*, Schwann's sheath presents an oval nucleus, at either pole of which lies a little granular protoplasm. The nucleus occupies a depression in the medullary sheath. Only in fishes are several nuclei found in a single internode. The nuclei of Schwann's sheath are best seen in preparations stained with carmine or aniline colours or in osmic preparations; in the latter they appear greenish-grey (figs. 41 and 45).

Lastly, each fibre is loosely invested by a delicate coat, the **adventitial sheath** (sheath of *Henle*); fibrillar or perineural sheath. It consists of



a thin membrane in which delicate longitudinally-running fibres seem to lie (presumably plaits in the membrane). The nuclei which lie on this sheath and stain out conspicuously with fuchsin are regarded as belonging to endothelial cells which clothe the sheath. A lymph space lies between the adventitial sheath and Schwann's sheath; but probably the adventitial sheath is not closed in completely on all sides.

[The endothelial sheath, which invests the fibres and provides a bath of lymph in which each fibre lies, is a specially modified layer of the immediately contiguous connective tissue cells. It is seen best where it surrounds isolated fibres, whether medullated or not (*e.g.*, olfactory nerves). Within a nerve-fasciculus it forms part of the endoneurium. In the central nervous system its place is taken by neuroglial tissue.]

Nerve-fibres which possess all the elements above mentioned occur exclusively in peripheral nerves.

Axis-cylinders, the essential elements in the conception of nerve-fibres, are found without further investment in the grey matter of the central nervous system, and in end organs. They are, for the most part, very fine, and may consist of but a single primitive fibril (fig. 48).

Axis-cylinders surrounded by an extremely thin membrane, which may be regarded as the homologue of the sheath of Schwann, or possibly of the sheath of Henle,\* but without medulla, compose the greater portion of the sympathetic commissural cords. In these cords, however, as well as in the sympathetic plexus, not a few medullated fibres are to be found. Usually their medullary sheaths are thin. Numerous oval nuclei are disposed around the non-medullated fibres with their long axes in the direction of the fibre. These nuclei belong to the sheath of Schwann, which lies so close on the axis-cylinder that its membranous nature can be scarcely recognised. Remak's fibres appear to differ somewhat in behaviour from the axis-cylinders of medullated fibres. They may be best compared, perhaps, to the non-medullated fibres in invertebrates. It is probable, too, that the non-medullated fibres of the olfactory nerve are not absolutely identical with those of the sympathetic (*Tukett*). They frequently appear to divide and unite again in plexuses. This appearance results from the difficulty of isolating the fibres. They are supposed by *Boveri* to possess a delicate analogue of a medullary sheath, which, however, is chemically distinct, since it contains no myelin. Non-medullated fibres are also to be found in varying number in all the peripheral nerves of the brain. They occur most frequently in the nervus vagus. Scattered grey fibres are also to be found in all the peripheral cerebro-spinal nerves. To see these fibres well the sym-

\* [The membranous sheath which surrounds non-medullated fibres and carries numerous nuclei on its internal surface has been regarded usually as the homologue of the similar sheath which invests isolated medullated fibres; the sheath of Henle. It has been customary, on the other hand, to look upon Schwann's sheath as a membrane, possibly the investing membrane of the myelin cells, which cannot exist apart from the medullary sheath.]



pathetic nerve should be taken from the neck of a living or recently killed animal, placed in a weak solution of bichromate of potassium (1 in 200), stained in carmine, and teased out (fig. 46).

A very good preparation can be made by placing the Remak's fibres from the nervus vagus of a dog in a half per cent. solution of osmic acid for twenty-four hours. To obtain non-medullated fibres in as good condition as possible they should be taken from the branches of the plexus caroticus which issue from the ganglion cervicale supremum, or from the nerves of the spleen. The latter are the more difficult to find. Both motor and sensory nerves at their peripheral ends lose first their sheath of myelin and then their sheath of Schwann.

Medullated fibres destitute of Schwann's sheath are also to be found; all medullated fibres of the central nervous system belong to this class.

They are best seen after a small piece of white matter from the brain or spinal cord has been placed for twenty-four hours in a weak solution of

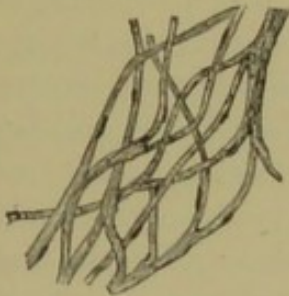


Fig. 46.—Remak's fibres from the sympathetic of the neck of a rabbit. *Carmine staining.* *Magn.* 200.

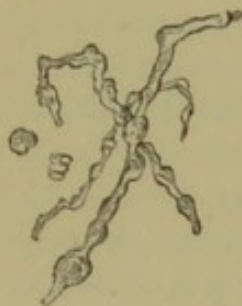


Fig. 47.—Central medullated nerve-fibre from the brain, without sheath of Schwann. *Magn.* 200.



Fig. 48.—Very fine varicose axis-cylinders from the bulbos olfactorius of the dog. *Magn.* 400.

perosmic acid (1 in 1000) and then teased. Such medullated fibres having no supporting investment, do not show a distinct border when they are teased out; but the medulla bulges ('varicose fibres') or breaks away from the axis-cylinder, leaving it free for a longer or shorter distance (fig. 47). The central medullated fibres also possess Ranvier's nodes, and structures similar to the cones of Lantermann, though they are very difficult to show.

The fine non-medullated, as well as the finest of the medullated fibres which have no sheath of Schwann, show the axis-cylinder beset with little swellings (varicose axis-cylinders). It might be concluded from this that the finest axis-cylinders are not invested with an axis-cylinder sheath (fig. 48).

No difference in structure between motor and sensory fibres has yet been detected; nor is it, as was formerly supposed, correct to say that motor fibres are uniformly larger than sensory; rather has *Schwalbe* proved that in general those fibres are thickest which have the longest course. So far as mammals are concerned, it appears that the fibres are larger in the larger animals, a conclusion in harmony with the statement just made as to



the relation of diameter to length. This law, however, is not universally applicable. Perhaps the abnormal fineness of some nerve-fibres is the cause, in certain cases, of inhibitory effects, for which an anatomical basis has been imagined to explain the neuropathic disposition (*Pick*).

[The size of a nerve-fibre depends upon other factors besides its length. Up to a certain point it varies (in a motor fibre) as the size of the muscle-fibre which it innervates, although in considering cases bearing upon this rule the fact that a motor nerve-fibre usually divides to supply a number of muscle-fibres must be taken into account. The relation in number between the fibres of a muscle and the fibres of the nerve supplying it is constant for each case, but varies widely for different muscles, from 1 nerve-fibre to 40 muscle-fibres in the leg, to 3 nerve-fibres to 7 muscle-fibres in the extrinsic muscles of the eyeball. Many more observations and numerous corrections are necessary before the laws which govern the size of nerve-fibres can be formulated. The quality of its action as well as the size of the muscle-fibre appears to influence the size of the nerve. The fibres going to the slowly-acting red muscles of the rabbit are smaller than the fibres supplying the more highly differentiated white muscles. Spinal motor and sensory fibres reach a diameter of about  $20\ \mu$  in the dog (*Gaskell*). Medullated sympathetic fibres are usually from  $2\ \mu$  to  $2.5\ \mu$  in diameter. At the first moment it might be thought that the fibres supplying plain muscle do not support the generalisations just made; but it must be remembered that their disposition is very different to that of the motor-fibres of striated muscle; instead of each fibre running straight from its nutritive cell in the spinal cord to its destination, it ends in a sympathetic ganglion in a 'distributive' cell from which a large number of fine non-medullated fibres proceed to the muscle. It is possible that in Auerbach's and Meissner's plexuses of the muscular coats of the intestine the process of subdivision is carried still further.]

In the spinal cord of many fishes a single conspicuous fibre is to be seen in the anterior column on either side, *Marthner's* 'colossal fibre' with a diameter of nearly 0.1 mm. So, too, in *Malapterurus electricus* the fibre in the spinal cord destined for the electric organ (also a single fibre on either side) is marked out by its considerable size. No medullated fibres are found in any invertebrate, nor are they present in cyclostomes or lophobranchii. *Rawitz* has found, however, in the nervous system of acephalæ a substance which may be ranked with myelin; and in the nerve-fibres of mussels, *H. Schultze* found globules and granules of a substance resembling myelin between the primitive fibrillæ. When treated with osmic acid it turned black. So, too, in embryos of early date all fibres are non-medullated; and the fact that they acquire their medullary sheaths by degrees (in some fibres only after birth) is the basis of one of the most important of anatomical methods.

The peripheral fibres in the puppy, for example, are already medullated at birth; but so unequally is the medullary sheath disposed that the fibres



look as if varicose (fig. 49). Perhaps the cause of Lantermann's cones is to be sought for in this bead-like deposition of medullary matter.

The chemical composition of the nerve-medulla differs at birth and in mature life. The medulla of new-born animals is not darkened to the same extent by osmic acid, and takes carmine and other stains more readily. The axis-cylinders are often remarkably large at birth, and the application of osmic acid gives them a greenish colour (*A. Westphal*).

It may now be regarded as certain that the axis-cylinder is an unbroken process of a cell, and that the cell is the genetic, nutrient, and functional centre of the fibre. The sheath of Schwann is probably mesodermal in origin, and must be reckoned, together with its nuclei, among connective-tissue structures. We have not yet arrived at any clear idea of the growth of the medullary sheath; it does not develop until the axis-cylinder is invested with the sheath of Schwann.

[The account of the structure of nerve-fibres given above makes it quite clear that the essential part of a nerve-fibre, the axis-cylinder, is an unbroken process of an epiblastic cell, the nerve-cell in the spinal cord or spinal ganglion. Spinal cord and ganglia were originally portions of the epiblast. The cord is formed by the involution of the neuro-epithelial tube. The ganglia are derived by delamination from rudiments which lie outside the rudiment for the cord. The epithelial cells of the embryonic cord throw out processes which seek, down through the mesoblast, for the muscle-fibres they are destined to supply, or else are elongated strands uniting the cell in the cord with a sister-cell in a sympathetic ganglion. The cells of the spinal ganglion throw out a process on either side. The distal process seeks a sensory cell. The proximal process works its way into the cord (*Beard*). It is almost impossible to suppose that the nerve-filament finds its muscle-fibre without a guide; perhaps the junction between nerve-cell and muscle-cell is effected very early, at a time when they are almost or quite in contiguity, and the subsequent elongation of the nerve-fibre is due to the change in situation of the muscle; at present the subject is beset with difficulties which will only clear up when fresh facts are brought to light. What is the origin of the myelin cells and other cells by which the axis-cylinder is ensheathed? In all probability the primitive neuro-epithelial cells fall into two groups. Some become nerve-cells; others, less favoured, serve for their support. These latter, again, exhibit a subdivision of labour. Some of them acquire a large amount of the fatty metabolite myelin, and, applying themselves to the nerve-fibres within the cerebro-spinal system, invest them with their cylindrical medullary segments. The formation of



Fig. 49.—Peripheral nerve-fibre from a new-born puppy, partially surrounded with myelin. *Magn.* 200.—*a*, Nucleus of Schwann's sheath.



the myelin sheaths from a succession of such cells, applied to the axis-cylinder, can be easily traced in peripheral fibres. The formation of the myelin sheaths of axial fibres has not been observed as yet, but there is no reason to believe that the process differs from that observed in peripheral fibres. If this is the case, the fibres of the white columns of the central nervous system must exhibit nodes of Ranvier, a question which has been much disputed. *Boll* and *Kölliker* say 'no.' *Schiefferdecker* and *Porter* describe and figure them. The investigation presents special difficulties, owing to the weakness of the axial fibres, unsupported as they are by sheaths of Schwann; but, according to *Porter*, the nodes of Ranvier can be exhibited in small portions of the white columns from the neighbourhood of the anterior fissures immersed for two hours (immediately after death) in a mixture of a 2 per cent. solution of osmic acid and 1 per cent. solution of nitrate of silver. The specimen is washed for five minutes in dilute caustic potash, and teased in dilute glycerin (2 parts of glycerin to 1 part of water). Other supporting cells constitute the connective tissue of the brain and cord, the cells of Deiters, or neurogleia-cells of various kinds. Have the myelin-cells of peripheral nerves a similar epithelial origin? *Vignal* is inclined to answer this question in the affirmative. He believes that they emigrate with the axis-cylinder from the central system. The sheath of Schwann would seem to be the outer cell membrane of the myelin-cell; the single nucleus indicating that each segment is formed from one cell only. It is difficult, however, to account for the absence of any such membrane around the myelin-cells within the cerebro-spinal axis, if both within and without the axis they are derived from similar epithelial elements. It is possible that the axis-sheath is the same cell-membrane on the incurved side of the myelin-cell.]

**Pathological Changes in Nerve-fibres.**—But few alterations in nerve-fibres due to diseases are known as yet; methods are certainly needed to enable us to recognise such changes. It is also very necessary to gain a clear understanding of the changes which take place in the healthy nerve after death, quite apart from the coagulation processes in the medulla which are observed to follow immediately upon the destruction of a fibre within the body. In twenty-four hours the myelin is gone from Ranvier's nodes, and is no longer homogeneous; in most fibres it is at the end of forty-eight hours broken up into round lumps, while in a few its place is taken by a fine transparent granular substance (*Köster*).

The most important form of **degeneration of a medullated fibre** yet observed, and the one most studied hitherto in detail, is that which results when a peripheral fibre is cut off from the nerve-centres (*cf.* p. 32). The first investigations in which this method was used were made by *A. Waller*, and hence the process is known as 'Wallerian degeneration.' If a peripheral nerve is cut across (the sciatic nerve is convenient for the purpose) one finds during the interval between the second and fourteenth day in a mammal (in cold-blooded animals the changes occur more slowly) after it has been hardened and coloured in osmic acid the following changes:



at first the myelin becomes cloudy, often swells considerably, and then breaks up irregularly. The segments do not seem to correspond to Lantermann's cones. Later it shows only scattered blackened drops and numerous colourless granules, Schwann's sheath being filled out in places only. The protoplasm and the nuclei appear to be increased. The axis-cylinder is broken into a succession of detached pieces of different length, often twisted or coiled; finally it disappears (fig. 50). In the last stage Schwann's sheath alone survives to represent the nerve fibre. It looks like a thin cord of connective-tissue; scattered groups of granules and a few myelin drops alone reminding us that we have to do with a tubular membrane. Multiplication of nuclei occurs by karyomitosis at first (*Tanagl*), but in the later stages the nuclei sometimes waste away. By the application of dinitrosoresorcin we can see that changes in the degenerated nerves set in very early, affecting not only the myelin but also the axis-cylinder. In twenty-four hours the axis-cylinder in the nerves of pigeons looks in places as if broken into several distinct pieces, while in many fibres it seems to have decayed completely (*Th. Beer*). According to *Monakow*, degeneration of the myelin sheath sets in throughout the whole length of the peripheral portion at one and the same time; and the farther from the cell the point of severance is, the more quickly does the process begin.

As the first result of section of peripheral nerves the degeneration advances, in the peripheral as well as in the central segment, only as far as the next node of Ranvier, where it seems to be stopped (*Engelmann*). While, however, in the central stump, despite its functional inactivity, no further changes occur for months, degeneration subsequently proceeds rapidly throughout the whole length of the peripheral portion of the nerve.

In the chromo-osmic method of *Marchi* (p. 30) we possess an extremely sensitive reagent for degenerated nerve-fibres. One of its great advantages is that in the section it reveals the degenerated fibres *in situ*, even after the tissue has been hardened. They can be distinguished by the appearance of black globules of varying size, which in longitudinal sections look as if arranged in rows. This method also shows very clearly that the degeneration extends to the central stump of a severed nerve. We may fairly assume that it will also enable us to detect changes in the myelin which do not necessarily imply the ultimate destruction of the fibre, that is to say, changes from which recovery is possible.

**Degenerative processes in non-medullated fibres** are known



Fig. 50.—Two fibres from the anterior roots springing from a softened spinal cord. *Magn.* 200.



in but a few cases, as, for instance, in the fine fibres of the cornea. *Ranvier* has observed in the *Remak's* fibres of peripheral nerves a multiplication of nuclei and the appearance of peculiar slightly-refracting granules as well as fat granules.

The progress of degeneration within the central nervous system when fibres are cut off from their centre appears to differ from that occurring in peripheral nerves in certain essential points not yet sufficiently understood.

While, for the first two or three weeks, the pathological changes of the central organ affect the nerve-fibres almost exclusively, presenting a passive image of degenerative decay, a process of gradually but steadily increasing activity makes itself felt in the intervening tissue; granular cells appear, and multiplication of nuclei and condensation of connective tissue occur. In a transverse section through the part of the brain or cord affected, the nerve-fibres untouched by this process are seen to be isolated and disconnected from one another. This proves beyond doubt that the further course of secondary degeneration is associated with a process of irritation in the intervening tissue, leading to a condensation and subsequent contraction of the whole part affected. How this process is inaugurated—whether by irritation set up by the decomposition-products of the nerve-fibre, by altered conditions of nutrition, or by change of position consequent upon the loss of the decayed nerve fibres—we are not in a position to state.

So far as concerns the intervening tissue, the histological process of secondary degeneration in the white matter of the brain does not seem to be the same as in the spinal cord.

Later, the process of **regeneration** may be observed in cut peripheral nerve-fibres, the first indications appearing in some cases at the end of eight days, sometimes much later—in two or three months. On the whole, the central idea of the process consists in this—the axis-cylinders of the central portions of the cut nerves constitute the foundations for the newly-created nerve-fibres, which grow through the scar and enter the old sheaths of Schwann, several nerves often entering a single sheath, along which their course to the periphery is directed. At first these newly-formed fibres are finer than the old ones, and the distance between the nodes is less. According to *Notthaft* the investment of the new axis-cylinder with medulla begins in from ten to eleven days, and proceeds from the centre outwards. It is not impossible that the elements of the peripheral stump, especially the proliferated nuclei, may take an active part in the rebuilding of the nerve, going, perhaps, to form the sheath of Schwann. *Korelew* describes the formation of new nerve-cells in the central stump from which new axis-cylinders develop and extend towards the periphery. According to *Kennedy's* observations fresh axis-cylinders are formed in the peripheral stump as well. These, however, only attain complete development after the nerve has reunited. A direct union of a cut nerve by 'primary intention' is impossible (*Krause*).

The regeneration of non-medullated fibres has been studied in the cornea (*F. Schultz*).

Regeneration of fibres in the central nervous system with restora-



tion of function never occurs, in the higher animals at any rate. While the segments of a cut peripheral nerve grow together again, a cut central nerve-tract is for ever put out of action. Accordingly, every lesion of the central nervous system must heal with a scar of non-nervous tissue.

*S. Mayer* has proved that a continual replacement of nerve-fibres goes on normally in peripheral nerves; since fibres are always to be met with in conditions of de- and re-generation. This is especially the case in the nerves of the brown rat (*Mus decumanus*); but the same holds good of the peripheral nerves in man. *Kopp* found that in human cutaneous nerves the proportion of degenerating fibres might rise as high as 18 per cent. Only in the first half-year of life are they entirely absent. In advanced age and in poor conditions of nutrition the number of degenerating fibres, and more especially of empty sheaths, increases. In pernicious anæmia and similar grave derangements of nutritive function, degeneration of the nerve-fibres of the spinal cord is frequently met with. On the other hand, *Teuscher* finds that extreme cachexia is not accompanied by any corresponding decay of large numbers of nerve fibres. He admits, however, that hard work and the enforced activity of a nerve may favour such degeneration.

A peculiar form of disease to which peripheral nerves are liable is **segmentary degeneration**. It was first described by *Gombault* as a result of lead poisoning, and afterwards in connection with alcoholic neuritis. In these cases the nerve is not diseased throughout, but only in certain segments, which alternate with others that remain quite normal. Further, the disease affects only the myelin sheath and the sheath of Schwann, while the axis-cylinder appears at first, at any rate, to remain intact. Lastly, the products of the destroyed myelin are not large drops, but little groups of fatty granules. Later, the axis-cylinder decays, and the final stage is the same as in ordinary Wallerian degeneration.

There is, besides, a simple atrophy of the nerve-fibres, in which they grow thinner, and the myelin sheath, which is the part most strongly affected, ends by disappearing altogether (*Köster*). This process is often met with in fibres which have suffered no direct injury, but atrophy in consequence of the destruction of the cell-group to which they are anatomically and physiologically related (see *Monakow's* works on the subject). This may be rightly named 'tertiary atrophy.'

Another form of nerve-degeneration is associated with partial **hypertrophy of the axis-cylinder**. This is hardly ever found except in central fibres, and is usually a sign of irritation, as, for instance, in myelitic

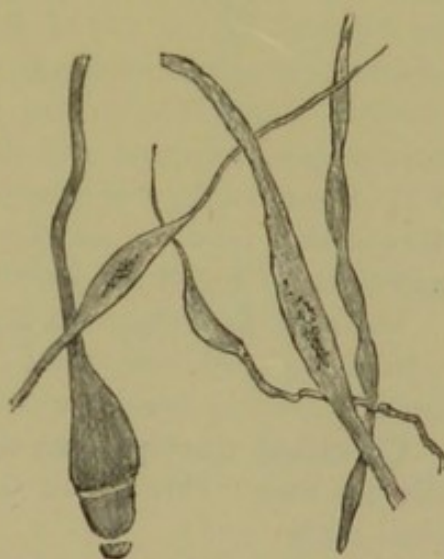


Fig. 51.—Several forms of hypertrophic varicosity of axis-cylinders from softened foci in the spinal cord. *Magn.* 200.



and encephalitic lesions ; often, too, in neuro-retinitis the optic fibres of the retina, which are just as well considered as central fibres, suffer beaded enlargement. It may, however, be set up without any direct process of irritation, merely by the absorption of lymph (*Rumpf*). This is known as œdematous swelling of the nerve fibre. It occurs in myelitis, due to compression. It is sometimes accompanied by swelling of the myelin, and in the final stage we find spaces in the transverse section corresponding to the swollen and decayed fibres.

In less severe conditions the axis-cylinder shows only slight swellings (varicose axis-cylinders, fig. 51). In advanced stages it may for a considerable distance be swollen out to six times its normal diameter, when it usually begins to exhibit transverse cleavage. This swelling appears soon after the irritation is set up. In a man suffering from a gunshot wound in the spinal cord *Charcot* observed it twelve hours after the infliction of the injury. In the foci of disseminated sclerosis the axis-cylinders often present perceptible swellings (*K. Hess*). Fine granules of fat, usually arranged longitudinally, are often found in the enlarged pieces ; their presence places beyond a doubt the degenerative character of the process. In fibres presenting this inflammatory change the separate swellings of the axis-cylinder may be so charged with fat granules as to present the appearance of fattily degenerated cells (*Unger*).

The medullary sheath of the spinal cord is also in some cases of myelitis considerably thickened (*Leyden*). It is necessary, however, that one should carefully exclude cases in which the enlargement occurs post-mortem.

**Calcified nerve-fibres** which are not the processes of calcified nerve-cells are rare. *Förster* saw calcified fibres in the lumbar swelling of the spinal cord.

*H. Schuster* and *Redlich* have described, under the name of **hyaline degeneration**, a form of hypertrophy in which the nerve-fibre becomes coarse and uneven. Numerous transparent and highly-refracting balls are found along its course ; they are of different sizes and entirely homogeneous in character, and they turn bright red on the application of eosin. The remnants of the decaying nerve occupy the intervals between them. The axis-cylinders remain intact. The hyaline lumps can be stained in almost any staining agent, but the colour fades very quickly.

### (b.) NERVE-CELLS.

The nerve-cell (ganglion cell or neurocyte) may be regarded as physiologically the most important part of the neuron, and therefore of the whole nervous system, the nerve-fibres being primarily mere conductors of excitation. Anatomically, also, the fibres must be treated as processes of the cells.

We may define a nerve-cell anatomically as a cell from which a nerve-fibre arises ; but it is often far from easy to determine under the microscope the nervous or non-nervous nature of a cell in the nervous system.



The primitive form of a nerve-cell is the sphere; from this, by the prolongation of one of its axes, a pyriform, by the prolongation of both, a fusiform body is produced. Never, however, is one diameter of the nerve-

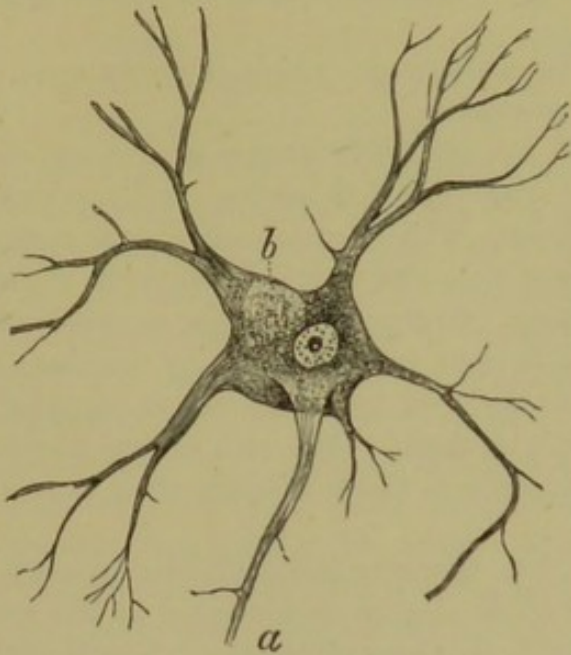


Fig. 52.—A cell from the anterior horn of the human spinal cord. *Magn.* 150.—*a*, Axis-cylinder process; *b* clump of pigment.



Fig. 53.—A cell from the anterior horn of the spinal cord of the pike. *Magn.* 150.

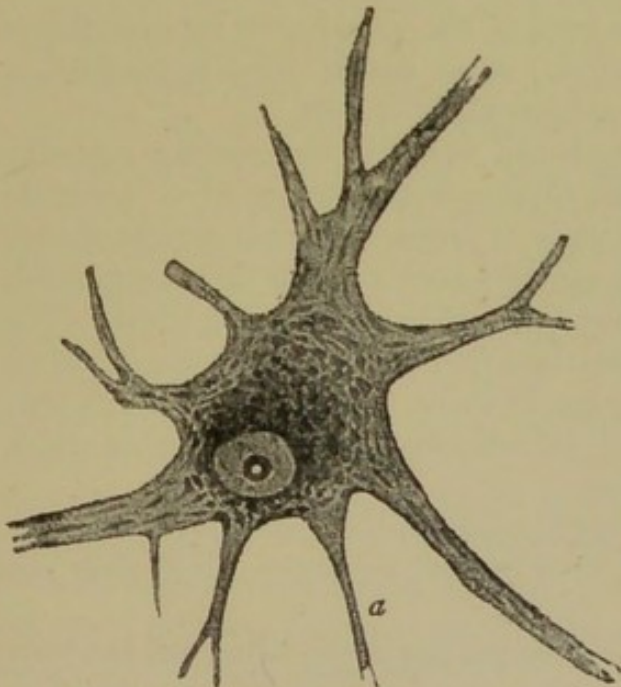


Fig. 54.—A cell from the anterior horn. *Nissl's staining.*

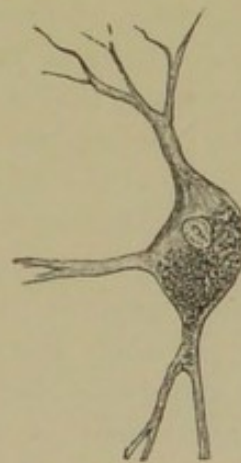


Fig. 55.—A pigmented cell from the substantia ferruginea. Human brain. *Magn.* 150.

cell greatly diminished (as in tessellated epithelium) or greatly increased (as in muscle-fibre).

So it comes about that from every nerve-cell one process at least, but



usually more than one, originates, which (by the gradual renewal of the cell-body) alters, but never completely obscures, the globular or spindle shape of the cell. Variations are occasionally met with; such are, for example, the cells with lobe-like appendages found in the spinal ganglia of the tortoise.

All nerve-cells possess a granular protoplasm, which is for the most part prolonged some distance into the processes.

In the interior of the nerve-cell is a relatively large clear nucleus, round or oval, or occasionally angular with rounded angles, and presenting, besides, a characteristic granulation, which occasionally constitutes a distinct network; an unusually large nucleolus is found within the nucleus; in this often a nucleolus is to be seen. In many nerve-cells, especially those of the cortex cerebri, the nucleus is seen to be crossed by one line or by several. This peculiarity was first observed by *Roncoroni*, in preparations stained in methylene-blue by Nissl's method. Cells with several nuclei are also found among the sympathetic cells of many animals, such as rabbits, guinea-pigs, etc.

A peculiarity of structure (fig. 54), formerly called fibrillar striation, on the authority of *Max Schulze*, is often clearly recognisable in the actual cell-body or protoplasm of the cell. By the application of Nissl's method (p. 16) or one of its modifications, the cell-body is seen to consist of a colourless or almost colourless basis substance containing very large numbers of scattered coloured corpuscles. In spite of great variation in shape, size, number, and arrangement, the granules so far correspond in cells of the same kind (those from the anterior horn of the spinal cord, for example, or the Purkinje's cells of the cerebellum) as to enable *Nissl* to establish a number of characteristic types for certain kinds of cells.

These coloured corpuscles (which are variously designated: granulae, Nissl's corpuscles, Nissl's cell-bodies, chromatin bodies, tigroid or basophile bodies, etc.) may be arranged in clots of irregular shape, groups, chains, spindles, etc. In most cases they can be traced for some distance into the process; generally they are spindle-shaped and lie along it lengthwise. The axis-cylinder process alone is free from them from the very beginning (fig. 54a).

A corpuscle of this kind, triangular in shape, is often affixed by its base to the nucleus (forming the 'cap of the nucleus'), or to the point at which a coarse protoplasmic process divides.

The name 'granule' is hardly appropriate, as the corpuscles themselves consist of extremely fine granules in a ground substance which does not stain with methylene-blue.

The pre-existence of these Nissl's corpuscles in the living cell has been repeatedly contested; *Held*, for instance, regards them as decomposition-products evolved in the process of hardening. Be this as it may, the regularity with which they make their appearance in certain parts of the cell, and the variations they exhibit in certain conditions (abnormal conditions especially), are circumstances which constrain us to consider them with close attention. They are insoluble in alkaline fluids.

These granules, spindles, etc., sometimes give the protoplasm of the cell



the appearance of a very clearly marked striation. Formerly it was thought that the fibrillæ seen in the axis-cylinders entered the cell and were there in some degree enveloped (*M. Schulze*), and that by the methods above mentioned the fibrillar structure of the nerve-cell could be exhibited.

The existence of these primitive fibrillæ in the cell-body may be looked upon as extremely probable, but they are situate in the so-called 'achromatic' substance between the coloured corpuscles. They can be made visible, for example, by the help of Delafield's hæmatoxylin (2 of hæmatoxylin in 200 of saturated solution of ammoniated alum, left exposed to the light for ten days, and then mixed with 100 of alcohol and 100 of glycerin. The mixture should be filtered and kept for some months before using). This fibrillar structure is, however, contested by many observers; *Lenhossék*, for instance, maintains that the ground substance is filmy or spongy, *Bütschli* that it is honeycombed.

*Held* is likewise of opinion that the substance of the nerve-cells and axis-cylinders consists of small longitudinal vacuoles with fine granules (neurosomata) embedded in the walls. Moreover, the recent investigations of *Flemming*, *Lenhossék*, and *Bühler* have shown that the structure of nerve-cells is far more complicated, and that they represent organisms with a relatively high degree of differentiation. Thus, in the cells of the spinal ganglia of many animals we can recognise a system of radial fibres, which start from a small corpuscle, the centrosoma, and must be regarded as distinct from the structural elements already described.

A simple method of showing the structure of the cell is as follows:—

From the anterior horn of the spinal cord of a freshly-killed animal take a piece of tissue about the size of a pin's head, put it on a slide and squeeze it out into an exceedingly thin layer by pressing a cover-slip upon it. Next put a drop of 0.5 per cent. watery solution of methylene-blue at the edge of the cover-slip, and lift the latter slightly, so as to bring the fluid in contact with every part of the preparation. In from half a minute to a minute take off the superfluous moisture with blotting-paper and carefully remove the cover-slip, leaving the film of tissue, as intact as possible, adhering to either cover-slip or slide. Expose it to the air for five or ten minutes, and as soon as it is dry mount in Canada balsam or dammar varnish (*Thanhoffer* and *Kronthal*).

It is exceedingly difficult to distinguish small nerve-cells from other cellular structures. No such difficulty exists in the case of the larger ones, which are amongst the largest cells in the animal kingdom. They attain to a size of 0.1 mm., and even more in diameter in mammals; and in many fishes they are larger still (see p. 152).

Other characters by which the nerve-cells may be recognised are the following:—

Many of the larger nerve-cells, such as the pyramidal cells from the cortex cerebri, the cells of the anterior horn or of Clarke's columns in the spinal cord, contain a little heap of light yellow granules, regarded as a lightly-stained fat-like 'pigment' substance. Usually the pigment is accumulated on one side of the cell near a process (fig. 52). A dark-brown



pigment is less common; it may almost fill out the cell-body, so that the nucleus remains as the only clear spot, and may extend for some distance into the processes (fig. 55). Such pigmented cells are grouped together in masses in two situations in the brain, the substantia nigra Sæmmeringi and the substantia ferruginea. They are scattered in other situations, as, for instance, the border of the vagus nucleus. Strongly pigmented cells are to be found outside the brain in the spinal ganglia and the ganglia of the sympathetic. No relation seems to obtain between the general abundance of pigment and the pigmentation of the nerve-cells. Many large cells, as, for instance, Purkinje's cells in the cortex of the cerebellum and certain small cells, always remain devoid of pigment, as do many of the smallest cells.

The chemical nature of the pigment is not yet understood. The clear pigment stains dark with osmic acid and often with Weigert's hæmatoxylin method. The dark pigment of the human brain becomes lighter when treated with concentrated sulphuric acid. A pigment is found in the nerve-cells of fresh-water molluscs, which turns green, blue, and finally indigo on treatment with concentrated sulphuric acid (*Buchholz*), and in acephalæ there exists a brownish-yellow pigment which turns, on the application of this reagent, a deep olive-green (*Rawitz*).

Pigmented nerve-cells are rare in animals. They are found hardly anywhere except in the spinal ganglia, the ganglia of the sympathetic, and (in many mammals) in the large nerve-cells of the spinal cord. Especially noticeable are the large black pigmented cells in the ventral part of the spinal cord of *Amphioxus lanceolatus*. In many amphibious animals two large cells (posterior cells) filled with fine granular pigment are found on the dorsal periphery of the embryonic cord. They disappear at a later stage of development.

The pigment granules in the human nervous system appear, even under the highest magnification, always round or roundly angular.

The pigment does not appear everywhere simultaneously. First (towards the end of the first year) comes the dark brown pigment of the substantia ferruginea, and next (between the third and fourth years) the dark pigment of the substantia nigra and the vagus nucleus. In Man alone is this dark pigment found in the central nerve-cells. The amount increases rapidly, and is fairly constant from the beginning of puberty onwards.

With the light pigment it is different. It appears in the spinal ganglia about the sixth year, in the spinal cord about the eighth, and may not be present in the cortex of the brain until nearly the twentieth. It has no fixed maximum, but continues to increase steadily up to advanced age (*Pilcz*).

Nerve-cells are further characterised by the behaviour of their nuclei towards hæmatoxylin. If one stains a section with alum-hæmatoxylin (p. 17), all nuclei, except the nuclei of nerve-cells, assume a deep blue colour; but even the largest nerve-cell nuclei presents merely a blue-grey tone.



Nerve-cells are not invested by any proper cell-wall. In some places, such as the spinal and sympathetic ganglia, and in the accessory auditory nucleus, they are enclosed by capsules of epithelial cells, through which the processes, which are usually simple, come out (fig. 56). According to *Max Schulze*, the cells on the auditory nerve of the pike are invested with a myelin case.

The forms assumed by nerve-cells and their processes are observed in detail, partly in sections prepared by the several methods already described, partly in preparations of isolated cells, or in tissue flattened into a thin layer (p. 145). For separation, pieces of grey matter from the anterior horn of a spinal cord, as fresh as possible, are macerated in the following way:—They are placed in a weak straw-coloured solution of bichromate of potassium for two to four days, or by *Ranvier's* method in a mixture of one part absolute alcohol and two parts water. A little carmine or fuchsin

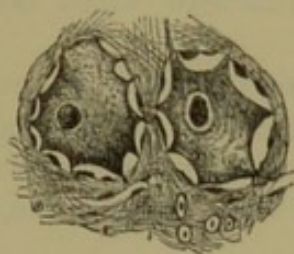


Fig. 56.—Two cells from a human spinal ganglion. They have shrunk away from their capsules, on the inner surfaces of which the nuclei which line them are seen. Each point of the cell which remains connected with the capsule looks like a process. *Magn.* 200.

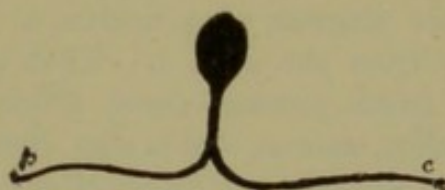


Fig. 57.—Diagram of a cell from the spinal ganglia. The peripheral and central processes unite and form a single stem shortly before their junction with the cell.

may be added directly to the macerating fluid. *Lavdowsky* recommends magdala-red or methyl-blue II. for the purpose. The larger cells with their processes may then be easily isolated with the aid of a simple microscope; it is best done in a drop of 0.5 per cent. perosmic acid. Fairly good permanent preparations may be made by spreading out the deposit containing the isolated cells on an object-glass, allowing it to dry, and covering with dammar varnish. Cells may also be easily isolated after the tissue has lain for fourteen days in a 0.1 per cent. solution of osmic acid.

The method of silver impregnation is, however, the only one which helps us to a clear understanding of the behaviour of the processes.

The number of processes given off by a nerve-cell varies, but, unless we include very fine branches, it seldom exceeds eight. Apolar nerve-cells seem to be physiologically inconceivable. They are to be looked upon either as developing cells or as artificial products. Unipolar cells are very



rare; most of them, like the cells in the spinal ganglia of mammals, may be looked upon as bipolar cells, the processes of which unite before they join the cells. *Ranvier* has proved that this is the case with the unipolar cells [of the spinal ganglia] which have a single T-shaped process.

The higher we ascend in the animal kingdom and the more highly-developed the nervous system, the richer in processes do the nerve-cells become, and the finer is the ramification of the dendrites, and possibly of the collateral branches of the axis-cylinder process also. This is easily proved by means of sections of homologous parts of the central nervous system. For example, one may compare the anterior horn-cells of fishes, which are usually bipolar (fig. 53), with the stellate cells of mammalia (fig. 52), or the pyramidal cells from the cortex of the cerebrum in different classes of animals. It stands to reason that the greater the number of conducting paths by which the nervous elements are bound together, the more complicated and varied will become the functions which they are capable of carrying out.

In the diagram of a neuron on p. 149 we see two kinds of processes starting from the cell, I. That marked *a* is designated axis-cylinder process (stem-process, nerve-process, chief-process, neurite, neuraxon, neuropodion, neuron, and is also known by many other names); the others are called protoplasmic processes or dendrites.

The axis-cylinder process has certain characteristics which enable us to recognise it in many nerve-cells, especially by the silver method of impregnation, but in a large proportion it is difficult or impossible to pick it out. There is seldom more than one axis-cylinder process, cells with two or more (bipolar or multipolar cells) having been met with as yet in but few parts of the central nervous system and spinal ganglia. The distinguishing marks of an axis-cylinder process are its origin from a small cone based upon the nerve-cell itself (fig. 58, *a*), or on the beginning of a protoplasmic process; a distinct projection of cell-protoplasm (not visible by the silver method) and its more homogeneous and hyaline character (figs. 52 and 54), due to the absence of chromatin filaments (*Schaffer*). Throughout its course it is smooth and sharply defined 'like a black thread.' The protoplasmic processes, on the other hand, originate by gradual attenuation of the cell, divide dichotomously or antlerwise, and sometimes present knots and irregularities in the branches. In some preparations they are marked by curious 'frostlike roughnesses'—fine thorns (gemmulæ, pyriform appendages), but this appearance is probably due to defective staining [*cf.* p. 155]. By strong magnification we can detect, along the course of the even thread, small granules of different colour which have no connection with it.

The axis-cylinder process may give off a varying number of more or less delicate side-branches (collaterals, fig. 58, *c*), and it finally breaks up into the arborescent system. In most cases it becomes a medullated fibre, invested from cell to arborescent system with a myelin sheath. The collaterals may also be so invested.

There are other nerve-cells in which the axis-cylinder process, instead



of passing over into an independent nerve-fibre, ramifies immediately, breaking up into an exceedingly rich network (fig. 59). These are called cells of Golgi's second type, or simply Golgi's cells. It is obvious that in cells of this sort the axis-cylinder process must lose more or less of its distinctive character, and, consequently, be hard to recognise. It may

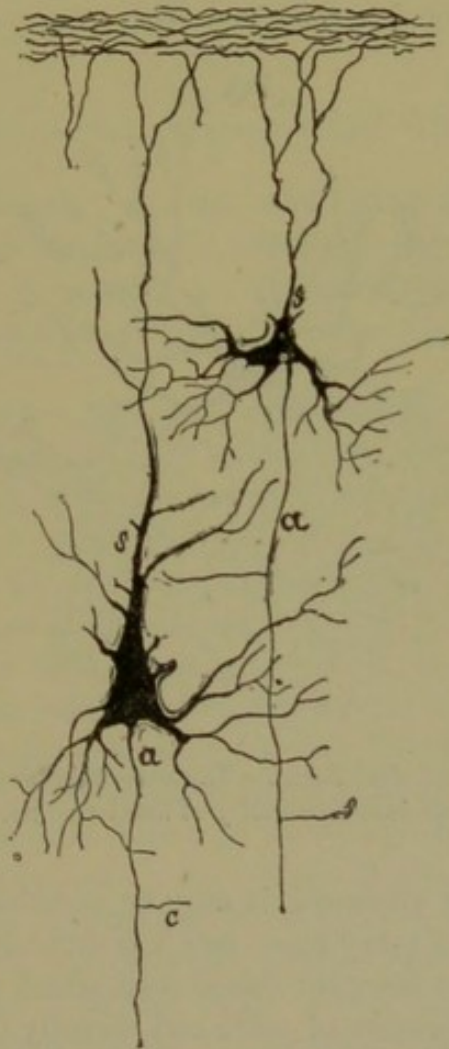


Fig. 58.—Two pyramidal cells from the cortex cerebri of a new-born puppy. *Silver prep.*—*a*, Axis-cylinder process; *c*, collaterals; *s*, apical process. The rest of the protoplasmic processes are not represented in the drawing.

even be questioned whether a sharp line of demarcation can be drawn between the two classes of cells (*Masius* and others). The distinction is still further obliterated by the fact that the ramifications of a protoplasmic process may pass over into a medullated fibre (*Lavdowsky*). The difference is best seen in carmine-stained preparations of the large Purkinje's cells of the cortex of the cerebellum.

The existence of apolar cells—that is, cells with no axis-cylinder process—is (to say the least of it) open to doubt. There may be adendritic nerve-cells, that is, cells with no protoplasmic processes. The cells of the spinal ganglia are, perhaps, of this character; but in them the lack of dendrites is compensated by the possession of two axis-cylinder processes (fig. 57). The large round cells in which the cerebral root of the nervus trigeminus



takes origin were regarded by *Golgi* as unipolar adendritic cells; but *v. Gehuchten* and others have demonstrated their multipolarity by staining the dendrites with nitrate of silver.

Anastomosis between different nerve-cells or different branches of the same, which has often been described (as by *Dogiel* quite recently), probably does not exist at all, or is only found as an abnormality. Investigations by the method of impregnation with silver, in particular, tend to discredit it.

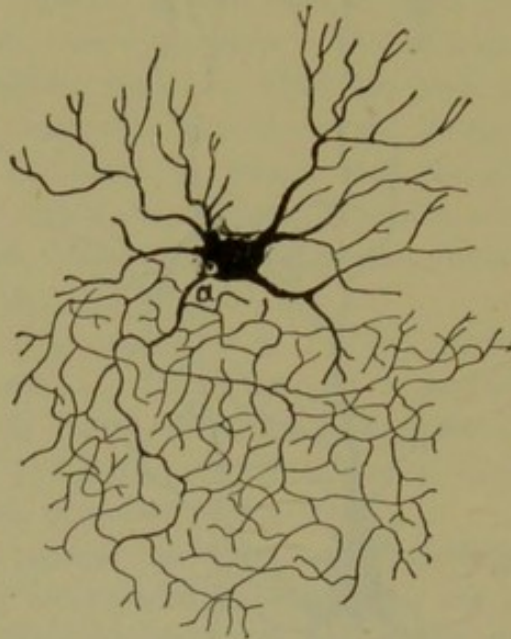


Fig. 59.—Golgi's cell (after *Andriezen*).—The axis-cylinder process, *a*, breaks up at once into a quantity of fine branches.

[Whether normal or abnormal it may be occasionally demonstrated in the case of nerve-cells of every class, and it is difficult to believe that none of the sympathetic fibres from the spinal cord, which presumably commence as the axis-cylinder processes of cells, end directly in 'distributive cells' of sympathetic ganglia.]

Other important facts concerning the behaviour of living nerve-cells and their processes have been discovered by the use of Ehrlich's method of introducing methylene-blue into the circulation (*Retzius*, inter alios).

A quite distinct kind of nerve-cell is found in many situations, as, for example, the retina, the olfactory bulb, and most abundantly in the nuclear layer of the cerebellum. The statements made with regard to nerve-cells are not applicable to these so-called **granule** cells (or myelocytes, as *Robin* calls them). They consist almost exclusively of granular nuclei of 5 to 8  $\mu$  in diameter, without any strongly refracting nucleolus. Their protoplasm is very scanty. Usually the processes and cell-protoplasm are not visible; in no case can the very fine processes be followed far (fig. 60). The method of staining with nitrate of silver throws some light upon the behaviour of these granules, which are certainly not all of like value, as I shall presently show in treating of the cerebellum. In fig. 60 they are seen to consist of a round cell-body with a sharp, delicate



axis-cylinder process originating from it. We further observe several dendritic processes, which soon break up and end for the most part in crooked, claw-shaped ramifications. The nuclei stain strongly with hæmatoxylin. This is a reason against regarding them, as is often done, as of

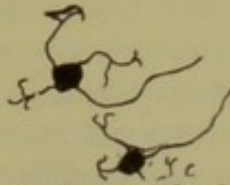


Fig. 60.—Granules from the granular layer of the cerebellum.

equal value with nerve-cells. On the other hand, they do not completely agree in structure with other tissue elements,—the connective-tissue cells, for example,—nor is it possible to imagine what might be the use of such heaps of non-nervous elements in so many places in the nervous system.

It is well to consider a 'granule' as a peculiar sort of nerve-cell with definite functions proper to itself. We can even discover certain transitional forms which link it to the ordinary nerve-cell. Granules are found in invertebrates as well as vertebrates. It has been suggested that they are nerve-cells which have remained rudimentary (*Chatin*); though it is hard to understand how such extensive layers of tissue-elements could have been arrested in one of the earliest stages of development without falling a prey to some process of retrogression, as superfluous ballast.

*A. Hill* sees in each granule a minute (receiving) nerve-cell by the intercalation of which a connection is established between a twig of the end-branching of a sensory fibre and the collecting protoplasmic processes of a motor (despatching) cell. He thinks it possible that the true conception of a complete neuron should include, in addition to protoplasmic processes, trophic cell, axis-cylinder process and its end-branching, the granules in connection with the twigs of the branches.

Among cellular elements in all likelihood nervous, though not yet certainly known to be so, we must reckon the cells which are present in large quantities in the substantia gelatinosa Rolandi of the embryo. They can seldom be exhibited in the adult.

[Each typical granule, although small, is just as perfect a nerve-cell as a cell of Purkinje or a motor cell of the anterior horn, and a consideration of the wide distribution of the granules throughout the central nervous system shows that they are equally as important as the larger nerve-cells. Probably a granule is an essential element of every 'nerve-couple.' Whether or not a granule is to be considered as a neuron depends chiefly upon whether the germ-cell or neuroblast from which it arises is from an early period isolated from the neuroblast of the larger cell with which it is in relation. It is possible that the nuclei of the granules are derived as daughter-nuclei of the cell with the end-branching of which they are in connection, or even that the reversed relation holds good. If this is the case, our conception of a complete neuron should include a nerve-cell, its axis-cylinder process with its end-branching, and the granules connected



with the terminal twigs. The neuroblasts of the granules are from an early date independent; each granule, with its protoplasmic and axis-cylinder, has, unless the hypothesis of the complex neuron be adopted, as much claim as any of the larger cells to be treated as a neuron.]

Widely divergent views are still held with regard to the **histological meaning of nerve-cells**. It has even been denied that they are cells (*Arndt*), and hence the name 'nerve-corpuscle' was proposed. We are not yet in a position to bring the varieties in shape, size, and pigmentation of the cells which we have already described into association with their physiological actions, still less can we account for the variations in the arrangement of their processes.

The variations in the pigmentation of the cells would seem to give us a clear indication of their functions, or at any rate of the special features of their metabolism; but unfortunately, as yet, we do not understand this hint.

With regard to the size of cells, we know that, as a rule, thick fibres belong to large cells, and *vice versa*. If we may also assume that the longest fibres are the thickest, the largest nerve-cells belong to the longest tracts. This statement is certainly not universally applicable, but it may have, at any rate, a limited value for the cells of any particular region, as, for instance, the pyramidal cells of the cortex. Just in the same way it is certainly not without significance that all the large cells of the cerebellar cortex have a uniform diameter. The largest cells are found in fishes, on the dorsal surface of the medulla oblongata. In *Lophius piscatorius* they sometimes attain a diameter of 0.257 millimeter and are visible to the naked eye; the oval nucleus may measure as much as 0.07 mm., the nucleolus 0.034 mm. A striking peculiarity of these cells is that their protoplasm is frequently traversed by capillaries, which may divide even within the cell itself (*Fritsch*). These vessels must not be confounded with the blood-circulation erroneously supposed by *Adamkiewicz* to exist within the nerve-cells.

An especial effort has been made to discover a difference between sensory and motor cells; or, as they would be better called, the cells standing in direct relation to sensory and motor paths. Evidences of such differences should be received with great reservation. Assuredly there must be many cells which are neither motor nor sensory in the proper sense of the words, but purely trophic; and, lastly, there must be cells which, if one truly understood their functions, could not be ranged in any of these categories.

In the cells of origin of the motor nerves we have an example of the type in which the axis-cylinder process passes over directly into a medullated nerve-fibre. From this Golgi drew the inference that all cells included in his first category were motor cells, and that those in the second (the so-called Golgi's cells) were associated with sensory functions. This view is no longer tenable; on the contrary, the cells of the latter type appear to create functional relations between the nerve-cells in their vicinity, and are hence called cells of association (*Ramón y Cajal*, *Lenhossék*).

The difference of behaviour in neighbouring cells towards colouring



reagents, such as carmine and Weigert's hæmatoxylin ('chromophilous' and 'chromophobic' cells) justifies the conclusion that they differ in function (*Flesch* and others). Here again I would remind the student of the variations of colour in different cells produced by Nissl's staining method.

The hypothesis started by *O. Kaiser* deserves mention. According to this, the chromophobic cells of the spinal cord are situated in regions associated with secondary or automatic functions, and cells become chromophilous in proportion to the subordination of their activity to that of the brain.

While the value of the axis-cylinder process as a conductor of nervous excitation is generally recognised, opinions differ widely as to the function of the protoplasmic processes. *Golgi* and his school take the lead in denying their nervous character. They maintain that such processes fix themselves on to the glia-cells and the walls of the blood-vessels, and thence infer that their function is primarily trophic, to subserve the nourishment of the nerve-cells. *Nansen* went a step farther, and refused to concede to the nerve-cell itself any direct part in nervous functions, regarding it as a mere organ of nutrition. We are forced, however, to acknowledge the nervous character of the protoplasmic processes, as the facts adduced in favour of the opposite opinion have not been confirmed by experiment. Foremost among many proofs, we can point to the structure of these processes, which (at least at their starting-point) differs in nothing from that of the cell itself. Decisive, if proved correct, would be the observation, made as yet by *Lavdowsky* alone, that a protoplasmic process may pass over into a medullated nerve-fibre. We may take it as rule (subject to exceptions) that the axis-cylinder process transmits cellifugal, the dendritic processes cellipetal, impulses (law of dynamic polarity).

It must be particularly noted that the protoplasmic processes of a cell sometimes differ in behaviour in a manner so constant as to justify us in assigning to them a difference of function. Thus, in many species of animals, the mitral cells of the bulbus olfactorius have a single protoplasmic process which brings the sensation of smell to the cell. Again, in the pyramidal cells of the cortex the apical process directed towards the periphery differs, not only in origin but also in behaviour, from the other protoplasmic processes; whence we may fairly conclude that it has functions proper to itself alone. The assumption of difference in function gains support from the fact that in many nerve-cells one protoplasmic process develops much earlier than the rest. Fig. 61 represents pyramidal cells from the cortex of an embryo 11 centimeters long. The axis-cylinder process is distinguishable, though without collaterals, while of the others only the apical process can be seen, with the first indication of a fork.

To *Forel* first, and then in a great measure to *Monakow*, is due the credit of having paved the way for our present conceptions of the mutual relations of the nervous elements. *Forel* thinks that the processes of neighbouring cells grasp one another like the branches of contiguous trees, without continuity of substance, but he leaves us uncertain as to the



manner in which he supposes these branches to end. From a physiological standpoint it is not necessary to exact a direct continuity of cell-processes.

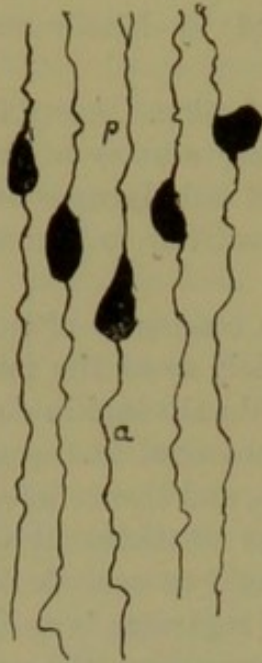


Fig. 61.—Five cells from the cortex cerebri of a human embryo 11 centimeters in length.—*a*, Axis-cylinder process; *p*, apical process with the first indication of a fork.

As far as our very elementary knowledge of physiological processes in the nerve-cells allows us to form a judgment, it may be quite sufficient for the purpose of the physiological transference of impulses to imagine an interlocking of the filaments without continuity; something like the super-position of the spiral fibre upon the sympathetic cell as described by *Ehrlich*. Apart from genetic reasons the appearances presented in successful silver or sublimate preparations are in favour of the latter theory. Individual cells with their rich network are coloured, but no anastomosis between neighbouring cells is shown. The study of the development of the central nervous system led *His* to a similar conclusion. He was convinced that continuity of nerve-tracts is not essential to the action of one fibre-system upon another; it is enough if the end-fibres of both extend into the same region and the intercalated substance be capable of transferring impulses. Besides the 'axis-tract' he assigns to each cell a 'con-

ducting-area.' By this phrase he understands the area immediately surrounding it and traversed by its protoplasmic processes (the dendritic processes). The provinces of contiguous nerve-cells interpenetrate, and may combine to form a common area.

We may formulate the view now in vogue by saying that no anastomosis or analogous connection exists between any two nerve-cells, but that each neuron is a distinct unit, capable of acting upon another by mere contact. The manner of this communication is known to us only in part.

Quite recently, however, various observers have expressed more or less doubt as to the correctness of the accepted opinion on the subject of neurons. *Held* would make a compromise between continuity and contiguity by assuming a 'concrecence' or intimate union between an arborescent process and a second neuron. *Apáthy*, again, holds that the primitive fibrillæ, starting from the periphery, pass without a break from cell to cell until they reach the periphery again.

[The invention of the chrome-silver method by *Golgi*, which first became generally known to neurologists in 1886, effected a complete revolution in the views held as to the nature of the elements of which the nervous system is composed. Individual cell-systems were seen in their entirety for the first time and with a diagrammatic distinctness which could not have been anticipated. The collaterals of axis-cylinders were demonstrated by *Golgi*, the basket cells of the molecular layer of the cerebellum by *Ramón y Cajal*,



the divaricating axis-cylinders of the granules of the cerebellum by *Pedro Ramón*, etc. By the use of Golgi's method our knowledge of the nerve-elements was multiplied many-fold; but the interpretation put upon the appearances obtained by this method will probably be regarded when the history of the subject comes to be written, as a strange retrogression. The advantage of the method lies in its staining one cell-system out of scores or hundreds which are left unstained; but in this selection lies its weakness also. Even if connection between homologous elements were to be looked for, the chrome-silver method would not show it; but, as we know, connection obtains only between heterologous elements; and heterologous elements are very rarely coloured in the same preparation. The various elements of which the nervous system is composed are therefore exhibited by this method as absolutely discrete; and the conclusion has been almost universally adopted by histologists that no nerve-network, no system of continuous nerve-paths in the sense in which *Gerlach* pictured them, exists in the grey matter. The *translator* has, in a series of papers, pointed out that such a conclusion is not inevitable. It may be avoided on the ground of the peculiar selection — the partial coloration effected by the silver. He has also pointed out that the silver-coloration (and the same may be said of methylene-blue) does not affect the conducting filaments or fibrils. The cell consists of various substances in which the fibrils are embedded, and it is in some of these constituents of neuro-plasm that the silver reaction occurs. In particular, he has shown that the various forms assumed by the 'thorns' on the dendrites prove that the softer staining substance has overflowed from the cell-plasm along the course of fibrils which the method does not reveal. Sometimes the thorns appear as rods with knobs at their ends (gemmules). Sometimes one dot or several dots are seen unconnected with the dendrite, but so placed as to indicate that they have been led into position by an invisible fibril. Occasionally the thorn is replaced by a filament of considerable length. The fibrils whose existence was thus inferred by the *translator* have been demonstrated in invertebrates by *Apáthy* using gold chloride. It appears to the *translator* that the nervous system consists of an absolutely continuous and universal network of fibrils of almost inconceivable richness; that the fibrils are collected by the dendrites of a nerve-cell and distributed by its axis-cylinder, small cells (granules) collecting the affluent fibrils, large (motor) cells collecting the efferent fibrils. The dendrites of the cells are naked, hence their ragged and varying appearance; the axis-cylinder processes are confined by a sheath, hence their clean-cut, thread-like definition. It is not improbable that the cytoplasm of the cell and its dendrites extends during life to a varying distance along the fibrils, and it is possible that the efficiency of the fibril as a conducting path, its condition of 'attention' or 'inhibition,' depends upon the extension or retraction of its cytoplasmic sheath. Perhaps the first of a sequence of rapidly-repeated stimuli (vibrations) induces the overflow of cell-plasm, or of some particular constituent of the cell-plasm, which favours the transit of its successors. Instead of the whole protoplasmic process being amœboid,



as imagined by Rabl-Rückhard, it is the cytoplasm only which is retractile along the course of the fibrils. The opening of a reflex path—the condition of attention—depends upon a certain alteration of the surface relations of the fibril and the cytoplasm which leads to the extrusion of the cytoplasm along the course of the fibril. Retraction of the cytoplasm accompanies and accounts for the opposite effect—inhibition. After death the cytoplasm retracts, and hence the continuity of the network can never be demonstrated by histological methods post-mortem.]

*Kölliker* observed certain end-ramifications of the fine fibre-network surrounding the cell in the form of exceedingly fine varicose fibres, generally terminating on its surface in small button-like swellings. *Ramón y Cajal* remarked a similar arrangement in the cerebellum.

The last and finest ramifications of the cell-processes, collaterals and arborescent systems alike, are closely interwoven in the grey substance, forming not so much a network as a felt-work, the neuropilema or neuro-spongium.

Some information has also been gathered concerning the phenomena of life in the nerve-cell.

Nerve-cells which survive removal from the animal to which they belong are best obtained from invertebrates. According to *Freud* the cells of the abdominal ganglion of the fresh-water crayfish may be examined in a living state in the blood of the animal. The living cell is seen to consist of a substance arranged in a network and apparently continued into the fibrillæ of the nerve-fibres, as well as of a homogeneous basis substance. In the nuclei of these cells *Freud* has seen a variable number of bodies assuming a variety of forms (for the most part they are longer or shorter rods, twisted or forked threads, and so forth), which, as long as the cell lives, undergo obvious changes in shape and place. *Wiedersheim* was able to follow under the microscope the changes in shape of the nerve-cell body in the brain of the lower crustacea.

*Rabl-Rückhard* has suggested, as a pure hypothesis, the possibility that the protoplasmic processes of nerve-cells which bear a part in the formation of the neuro-spongium are subject to amœboid variation, and that a broken thread of protoplasm corresponds to a broken thread of thought! *M. Duval* attempts to find an anatomical basis for the act of falling asleep by supposing that the arborescent systems which lie close to the nerve-cells of the cortex are then retracted.

*Ramón y Cajal* goes so far as to propound the hypothesis that intellectual exertion causes growth and increase of the collaterals and protoplasmic ramifications, which brings about fresh and more extensive inter-cortical relations. Although it is hardly possible to demonstrate any such increase, there is no doubt that the effectiveness of the brain as a machine is primarily due to the greater or lesser richness of the nerve-tracts situate in the processes and collaterals, by which the physiological relations of the nerve-cells to one another are brought about.

[*Gerlach* imagined the central nervous system as composed of a plexus. In the hypothesis that the network presented a multitude of routes of



varying resistance, physiologists found a simple basis for nervous action, and they pictured impulses as travelling along the lines of least resistance. The modern conception of the nervous system as consisting of discrete neurons is based upon appearances obtained by the chrome-silver method, and the method of injecting methylene-blue *intra vitam*; supported by the *a priori* consideration that the difficulties in accounting for anatomical continuity are perhaps as great as the physiological difficulties which surround the conception of a reflex mechanism composed of non-continuous elements.

The doctrine of discontinuity is commonly described as the 'neuron-theory,' although the term 'neuron' is equally needed to express the genetic and trophic unity of the nerve-cells and their processes, whether they are connected together or discontinuous. That all classes of nerve-cells may be united together by their protoplasmic processes has been shown by the *translator* and others; but this may indicate incomplete separation during growth.

The burning question at the present moment is:—Are the neurons independent, the nerve-currents being collected by the protoplasmic processes from the axis-cylinder ramifications of other neurons by means of gemmules (thorns), which may or may not be in actual contact; or do continuous conducting fibrils pass from cell to cell? The answer chiefly depends upon whether or not such fibrils can be seen within the cells, for it is difficult to imagine the ends of the fibrils as placed in conducting continuity by means of pads (gemmules) of the same cytoplasm which, when within the cells, serves as the insulating substance. Histologists are at variance on this subject, and it is almost premature to endeavour to reconcile the results of various methods. All agree that the cell consists of a chromophobic cytoplasm embedding chromophilous granules or masses, although it is uncertain whether these Nissl's corpuscles exist as such during life or are set free by an acid coagulation at death, or by acid reagents post-mortem. Almost all agree that the cell contains fibrils, but whether these constitute a reticulum (*Flemming, Lugaro, Marinesco*) or whether the fibrils are independent of one another (*Mann, Bühler, Bethe, Apáthy*) is a debated question. *Golgi* has demonstrated a coarse intracellular network, which does not seem to bear any relation to the fine reticulum referred to above. It is clear that the so-called chromophobic constituent of the cytoplasm must constitute a reticulum which, if coloured, would present a negative picture of Nissl's corpuscles. It may be that this contains a fibrillar reticulum which supports the traversing conducting fibrillæ; or, again, it is possible that the constituents of the cytoplasm coagulated about the fibrils make them appear to constitute a network.]

We are in possession of varied but conflicting evidence concerning the changes undergone by the cell during functional activity. We are told that the nucleus shrivels (*Hodge*), or swells (*Vas*), that the nucleolus removes from its central position to the periphery (*Magini*), that both cell and nucleus swell (*Mann*), and so forth. In the spinal cord of the frog after long faradisation, *Bohdan Korybut-Daszkiewicz* remarked that the



safraninophilous cells outnumbered the hæmatoxylinophilous by three or four to one.

*Nissl* and others have thought that in a state of rest the nerve-cell was reduced in size and presented a dark, pyknomorphous appearance, and that light, apyknomorphous cells indicated a state of fatigue. It is, however, safer for the present to be cautious in interpreting appearances of this nature.

The development of the nerve-cell is intimately connected with the behaviour of the epithelium of the central cavities, and will therefore be most fitly discussed in treating of the latter tissue. In this place I will merely observe that, according to *Vignal*, the first characteristic nerve-cells appear in the spinal cord, at a period corresponding to the tenth week of the human embryo. They constitute two groups in the anterior and lateral horns. The cells of Clarke's column do not appear until the fourth month.

**Pathological Changes in Nerve-Cells.**—While nerve-fibres, as far as we know, are subject to but few degenerative processes, the nerve-cells undergo in the living organism a great variety of pathological changes, always, unless recovery takes place, with the same physiological result, loss of function, and cell-death. Eventually the nerve-cell either disappears or some vestigial structure, depending for its character upon the nature of the change, alone remains to mark its situation.



Fig. 62.—Simple atrophy of a nerve-cell from the oculomotor nucleus. Human. *Magn.* 150.

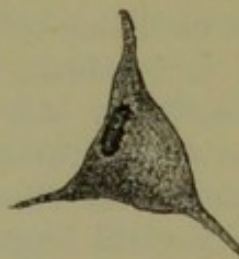


Fig. 63.—Commencing atrophy of a cell from the anterior horn of the spinal cord. Degeneration of the nucleus. *Magn.* 150.



Fig. 64.—Fatty-pigmentary degeneration of a pyramidal cell of the cortex cerebri. *Magn.* 150.

**Simple atrophy** of the nerve-cell may occur (fig. 62); owing to the shrivelling of the cell, first in one dimension and then in all, its processes are torn off at some distance from the cell. They often assume a corkscrew form. The nucleus becomes less distinct, and the last trace of the cell disappears, leaving occasionally an empty space. Sometimes the commencement of the atrophic process can be recognised in the nucleus, which shrivels, loses its smooth outline, and often takes up an eccentric position near the periphery of the cell (fig. 63). It becomes opaque, and takes readily certain stains, such as hæmatoxylin and nigrosin.

**Fatty degeneration** begins as an increase in the quantity of the pigment normally present (fig. 64). Consequently, it hardly ever occurs in



non-pigmented cells. Since the light yellow pigment has certain properties in common with fat, and is apparently a body related to fat, we often speak of a **fatty pigmentary degeneration**. The granular matter which accumulates in the cell in this form of degeneration is, however, much more like fat than pigment, and in the later stages of the disease the cell is simply filled with fat-granules. Since we cannot say how large a quantity of pigment a nerve-cell may normally contain, we cannot recognise the first stages of this degeneration. More and more fat accumulates in the cell until, in the later stages of the disease, it is simply a vesicle distended with fat which envelops the nucleus. Lastly, the nucleus disappears, the fatty vesicle breaks to pieces, and the fragments are absorbed. This degeneration is found in the several forms of chronic atrophy, such as senile atrophy, general paralysis, and the atrophy of drunkards. When a fatty cell has lost its processes it resembles an ordinary fat-cell, and it may, if it retains its nucleus, remain as such.

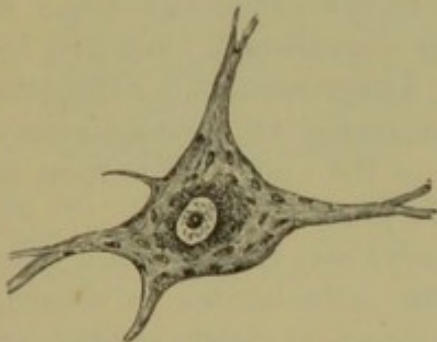


Fig. 65.—Granular degeneration of a cell of the anterior horn in myelitis. *Magn.* 150.

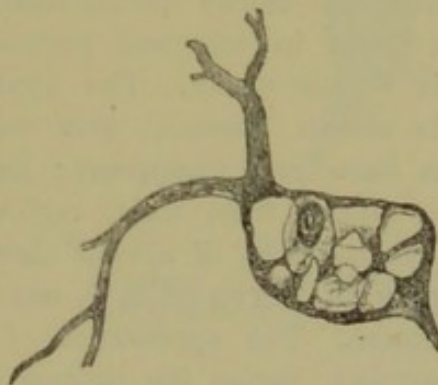


Fig. 66.—Cell of anterior horn, with ten vacuoles in myelitis. *Magn.* 150.



Fig. 67.—Colloid degeneration of a cell of the anterior horn in myelitis. *Magn.* 150.

There is a peculiar **granular degeneration** which indicates an acute process (fig. 65). The cell body is, in this condition, dotted all over with granules which are larger and rounder or more distinctly oval than in the degeneration last described, and give it somewhat the appearance of having been stained by Nissl's method. They stain with carmine. The distinctive features of the nerve-cell may for a long time remain unaffected. It should be particularly noted that the nucleus retains its normal character. *Pandi* observed this form of pathological change in cases of chronic bromide and nicotine poisoning.

Under the name of **homogeneous swelling**, *Friedmann* and *Schaffer* have described a form of degeneration, occurring in the cells of the cornu anterior in myelitis, in which the central portion of the cell is transformed into a homogeneous substance, while the marginal zone retains at first its normal granular character and the nucleus appears intact.

**Vacuole formation** is almost always, and indubitably in every case in which it reaches considerable dimensions, an indication of inflammatory processes. The number of spaces in the protoplasm varies;



there may be as many as ten, almost replacing the whole of the protoplasm, which persists only in the thin sediments between the vacuoles, and at the roots of the cell-processes. Nuclei and processes retain in these cases their normal appearance. *A. W. Campbell* regarded vacuole-formation in the nerve-cells as the expression of toxic degeneration. Attention must, however, be called to the fact that vacuoles may appear as the result of post-mortem changes. Near inflammatory lesions we sometimes meet with cells, the whole body of which is occupied by a great structureless hyaline drop of colloid. Such **colloid degeneration** (fig. 67) gives to the cells a peculiar globular form, such as is only possessed by a very few normal cells. The colloid drop stains deeply with carmine.

As the opposite of pigmentation, a condition may be mentioned in which pigment normally present in nerve-cells is lost, **depigmentation**. At the same time the protoplasm loses its characteristic granulation, the cell appears homogeneous, and stains but weakly with carmine, so that in sections the cells are hardly distinguishable from the basis substance. This change is found in sclerosed portions of the brain, and hence is termed sclerosis of nerve-cells. The hyaline degeneration described by some writers is almost identical with this depigmentation. Later, the cell changes in form and disappears; large masses of nerve-cells may in this way be missed from many regions of the brain. This form of atrophy is always the sign of a slow chronic process.

**Hypertrophy of nerve-cells** is not always easy to distinguish from post-mortem change. The appearance of the cell-substance is altered, usually becoming dim; hence the process is known as cloudy swelling or parenchymatous swelling; the nucleus is obscured. Only the higher degrees of this degeneration can be regarded as distinctly pathological; and it is an open question whether we should look upon this change as a well-marked form of degeneration *sui generis*. Similar changes have been found in senile and paralytic dementia, in other forms of feebleness of intellect, and also in extreme cases of inanition (*Rosenbach*). Varicose hypertrophy of single processes (the central processes of Purkinje's cells in the cerebellum, for example) seems to be rare (*Hadlich*). It must not be confounded with an alteration in the dendritic processes which has frequently been described in connection with various cases of poisoning (tetanus, alcohol, uræmia) under the name of varicose atrophy. This shows itself as a more or less regular chain of bead-like swellings along the processes in question. It starts from the periphery and proceeds towards the cell, and may even lead to irregular swelling of the actual cell-body (silver-colouring).

In many of the forms of degeneration described the processes of either kind tear at their commencement or at some distance from the cell (*Oettinger* and *Marinesco*). The student must be careful to distinguish between these injuries and such as are due to defects in the preparation.

**Calcified nerve-cells** (fig. 68) have been found in the spinal cord as well as in the cortex of the cerebellum and cerebrum. In the spinal cord they are found in the anterior cornua as the result of infantile spinal



paralysis and acute poliomyelitis; but they are more commonly found in the cortex of the cerebrum, arranged in groups, beneath superficial hæmorrhages (*plaques jaunes*), and after injuries in which the skull-case suffers directly and the brain indirectly, even when the brain appears to have escaped, so far as can be told at the time. In cases of softening of the cortex of the cerebrum, groups of calcified nerve-cells are often found embedded in masses of detritus and fat-cells. By absorbing calcium-salts they have acquired such power of resistance that while those around them have either perished or altered beyond recognition, they, or their skeletons, have maintained their position with hardly any change of shape. Hence

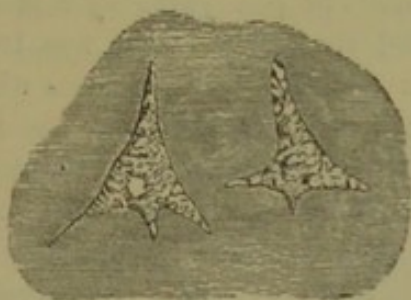


Fig. 68.—Calcified nerve-cells from the cortex cerebri beneath an apoplexy. *Magn.* 150.



Fig. 69.—A cortical cell (from the neighbourhood of a tumour) which has divided into a number of pieces. *Magn.* 150.

*Friedländer* considered calcification as characteristic of acute changes in nerve-cells. It will be inferred, without special explanation, that calcification is only a peculiar form of atrophy. Calcified nerve-cells are easily recognised even in the unstained preparation by their peculiar brilliance, as well as by the star-like arrangement of their processes. On the addition of sulphuric acid, they give off bubbles of carbonic acid gas, and crystals of sulphate of lime make their appearance. In preparations stained by Weigert's or Pal's method the calcified nerve-cells are black, with light nuclei.

Lastly, a series of changes in nerve-cells of a much more active nature must be mentioned. All, or almost all these, however, end in atrophy. It may also happen that, as the result of an irritative condition, the nucleus travels to the margin of the cell, or even lies for its greater part outside the cell-body. This is observed in *dementia paralytica* in the cells of the anterior cornua of the spinal cord (*J. Wagner*).

**Nuclear division** should be noticed. In inflammatory lesions changes in the shape of the nuclei are remarked. They are seen to be undergoing the kind of constriction which would end by their dividing. The process of nuclear division in inflammation was studied in detail by *Mondino* and *Coën*. They recognised karyokinesis in the large cells of the cortex of both cerebrum and cerebellum. In rabbits and guinea-pigs karyokinesis was recognised in the large cells of the cortex of both



cerebrum and cerebellum. Dogs are less favourable subjects for experiment. *Coën* found that the number of mitotic figures in the nerve-cells was largest in from four to six days after the infliction of the injury. On the other hand, *Fürstner* and *Knoblauch* could detect no mitotic figures in the nuclei of the nerve-cells. *N. Popoff* observed nuclear division of the nerve-cells in cholera as the expression of an inflammatory process. **Cell division** has been seen to occur as the consequence of inflammatory processes, either primary or resulting from the irritation set up in the neighbourhood of a tumour, or by artificial means. *Robinson* induced division in the cells of the sympathetic; *Ceccherelli* in artificially-produced encephalitis. A nerve-cell may divide into a great number of secondary cells which still, as a group, exhibit the original form of the parent cell (fig. 69, *Fleischl*).

Very important discoveries have been made of late years by means of the method of methylene-staining perfected by *Nissl*. This was to be expected, since it enables us to observe the more delicate processes within the cell. Indeed, it is no light task to keep pace with all that has been published on the subject. Considering that we must look for the actual conducting elements of the nerve-cell in the colourless ground-substance, it is obvious that the behaviour of *Nissl's* corpuscles cannot lay claim to the place of primary importance assigned to it by many writers. It is possible, not only for normal *Nissl's* corpuscles to exist in a cell functionally crippled by disease, but also for the cell to carry on its normal functions when the structure of the corpuscles is profoundly affected.

No satisfactory agreement subsists as yet with regard to all the points which concern the minute structure of the cell in disease. The most important change shown by *Nissl's* method is the resolution of the coloured corpuscles into extremely fine dust-like particles or granules, or their complete dissolution into a homogeneous mass, so that the ground-substance, otherwise almost colourless, is more or less deeply tinged with the colouring matter (chromatolysis). Chromatolysis never affects the whole cell at the same time and to the same extent; it may begin around the nucleus and spread towards the periphery (central or perinuclear chromatolysis); or it may originate in the periphery (peripheral chromatolysis); or, again, it may attack isolated spots in more arbitrary fashion and remain confined to them. Displacement of the nucleus frequently occurs; it leaves its central position, and moves, actively or passively, to the periphery of the cell.

If a peripheral nerve be cut through, very striking changes quickly ensue in its cells of origin. These are best observed eight or ten days after severance. According to *Marinesco*, they consist in a process of chromatolysis starting from the cone of origin, and displacement of the nucleus. Regeneration of both nerve and cell sets in at a later period, the latter appearing larger and darker during the process. In cases of poisoning from the most diverse causes, and in all states of disease, the nerve-cells undergo changes of various kinds, which can only be observed by means of *Nissl's* method. Whether each poison produces distinctive and charac-



teristic changes, as *Nissl* and others suppose, cannot be determined with certainty as yet.

In the same way we must admit with caution the distinction between primary degeneration and that which is secondary, *i.e.*, consequent upon the severance of a nerve.

It is improbable that regeneration of the nerve-cells destroyed by disease ever takes place, though it has been asserted that perfectly fresh nerve-cells may be formed in peripheral neurons.

There is, no doubt, a pathological condition of arrested or incomplete development of the nerve-cells, generally found in conjunction with idiocy or similar congenital defects. The distinguishing characteristic of such undeveloped cells is, according to *Bevan Lewis*, that the cell-body is indistinctly granulated and stains faintly with aniline colours, while the nucleus, which usually occupies an eccentric position, stains deeply. The number of processes is less.

## 2. NON-NERVOUS CONSTITUENTS ECTODERMAL IN ORIGIN.

### (a.) Epithelium.

The epithelium which clothes the cavities of the central nervous system, and that of the choroid plexus (of which I shall speak later on), is probably in some degree a vestige of the embryonic layer of cells known as the epiblast, which yields the material for the building up of nearly the whole nervous system.

What its further meaning may be in adult Man or animals we do not know; but since we wish to acquaint ourselves, in the first place, with the structure of the adult brain, we will begin by considering its behaviour in the developed organism and pass on to a survey of it in the embryo.

The adult human central nervous system is most unfavourable for the study of ventricular epithelium. Not only is it difficult to obtain from the human subject specimens of epithelium in a sufficiently fresh condition for observation before changes have set in, but it appears that the epithelium in question is better developed in lower animals than it is in Man, and also that in Man it undergoes, locally at any rate, changes in character after childhood.

The epithelial cells are not everywhere equally well preserved in the human nervous system. They are least altered in appearance in the central canal of the spinal cord, the floor of the fourth ventricle, and the aqueduct of Sylvius, where, in young persons, they may be seen as tracts of slightly-elevated cells, almost cubical in shape, and probably ciliated.

The cells are less perfect in other places, and the constant presence of cilia is so difficult to prove that their existence is doubted by some people.

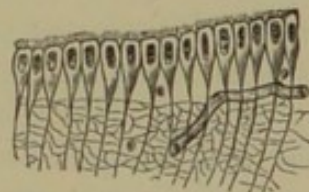


Fig. 70. — Ventricular epithelium of the frog.  
*Magn.* 200.



They are almost always arranged in a single layer, though *Lachi* avers that a deeper stratum is to be found in the neighbourhood of the posterior commissure.

The cells in the ventricular epithelium of the frog are particularly easy to exhibit. They are fairly high, ciliated, and possess a distinct nucleus. They are renewed from below, and the conical base of each cell is continued into a fine process which can be followed far down into the nervous substance towards the periphery. In addition to these processes, which occur in the epithelium of all animals, though sometimes in an atrophied condition, some short lateral processes are given off from the base of the cell.

The single layer of epithelial cells, together with the layer of connective tissue on which they rest, constitutes the so-called **ependyma**, which extends as far down as the distinctively nervous elements.

The ependymal cells are essential to the formation of the framework for the nerve-centres; indeed, in the early stages of embryonic life this framework is composed entirely of such cells and their processes. Then it is most clearly seen that each cell of the spinal cord sends out towards the periphery a long process, single at first but soon divided into two or more branches which end in a small knot on the free surface (ependymal fibres).

In the lower vertebrates this is their life-long condition, but in the higher mammals these radial supporting fibres disappear more or less completely, giving place to the scaffolding of neurogleia which I shall presently describe. The elements of this later tissue also take their origin from the ependymal cells.

In the spinal cord of even full-grown mammals the processes of the epithelial cells on the anterior margin of the central canal stretch as far as to the fissura anterior, while the 'posterior ependymal cells' with their processes form the septum posterius.

Even in very old dogs *Berkley* found ependymal fibres which extended as far as to the pia mater. He also draws attention to some peculiarly-shaped ependymal cells which he met with in the infundibulum in dogs. They are usually conical and send out a long process towards the periphery, while both cell and process give off numberless fine side branches at right angles. From the form thus produced he names them 'pine-tree cells.'

In dogs and rabbits numerous karyomitoses are found in the nuclei of the cells at birth and during the first few days, indicating a very active production of young cells.

Even when the plate of the medullary tube consists as yet of a single layer of epithelium we can see that the cells are of two kinds [*cf.* p. 39]. One kind, which bears the character of the palisade-like epithelium, is transformed later into the elements to which *His* gave the name of spongioblasts. The innermost of these afterwards acquire a covering of cilia and form the lining of the central canal and of the cerebral ventricles. Among the spongioblasts, but quite distinct from them, are roundish cells, the 'germ-cells,' which subdivide and form the elements called by *His* neuroblasts. On one side of these (which must be regarded as the rudiments of the nerve-cells) the protoplasm is drawn out into a process, the axis-cylinder process, short at



first, but quickly lengthening. At the same time, or even earlier, the neuroblasts sink away from the innermost layer of the now thickened medullary canal, to reach finally the place destined for the developed nerve-cells.

The process of the neuroblast continues to grow, sometimes to a very considerable length. The axis-cylinders of all nerves, peripheral and central, are in the first instance mere outgrowths from the neuroblasts. During the period of growth, that is, until the axis-cylinder process has reached its goal (a peripheral muscle-fibre, it may be), its free end is marked by a characteristic knobby swelling, the *cône de croissance* (*R. y Cajal*).

From the same rudiment and in similar fashion the permanent gleial scaffolding develops. Single cells, astroblasts (*Lenhossék*), move outwards from the layer of ependymal cells and are then transformed into gleia-cells.

According to *Schaper*, who impugns the views of *His* in particular, the germ-cells also originate from the epithelium of the medullary canal, and by moving outwards form a layer of indifferent cells (the mantle-layer of *His*). These subsequently differentiate into neuroblasts (afterwards nerve-cells) or spongioblasts (afterwards gleia-cells).

### (b.) Neurogleia.

It has long been recognised that there exists throughout the nervous system a tissue distinct from the purely nervous elements and the vessels. On the assumption that the principal function of this peculiar tissue was to supply a supporting framework for the organ, it was called 'supporting tissue'; but, from the first, anatomists felt difficulty in arriving at an exact histological appreciation of it, that is to say, in ranging it in the category of any known tissue. For this reason *Virchow* gave it the distinctive name of gleia or neurogleia, nerve-cement.

For a long while the view most generally accepted was that two distinct constituents went to form the neurogleia: (1) cells with many long processes, called Deiters' cells, which were supposed to be a form of connective tissue peculiar to the central nervous system; and (2) a fine fibrillar or granular basis substance.

But the conclusion once arrived at that the greater number, at all events, of Deiters' cells spring from the ependyma, the theory that they are of the nature of connective tissue becomes untenable, especially in face of the light thrown upon the subject by the use of the silver method of impregnation.

It became more and more open to question whether true connective tissue of mesodermal origin bore any part with the purely ectodermal gleia-tissue in building up the central nervous system. Modern methods of staining, such as Weigert's and Schaffer's, showed that the septa of the spinal cord (formerly supposed to be of the nature of connective tissue) are entirely composed of gleia. Nor could the apparent connection of gleia-fibres and connective-tissue elements be maintained. Observers fancied that they could discern the manner in which such gleia-fibres attached



themselves with conical bases to the vessels (figs. 77 and 78). This appearance was, as a matter of fact, fallacious; the processes do not attach themselves to the vessel at all, but stop a little short of it and unite with other processes to form a gleia network (see p. 173 and fig. 79).

*J. Schaffer* recommends a method for distinguishing the connective-tissue elements from the true neurogleia. He stains in acetic-acid-hæmatoxylin (p. 24), differentiates in solution of borax-ferridcyanide of potassium, and leaves the sections for several days in a very dilute solution of eosin. The neurogleia fibres then appear red, while the glutiniferous connective tissue remains brown.

For the study of the gleia-cells of the central nervous system it is best to take little pieces of the fresh brain or spinal cord, and macerate them

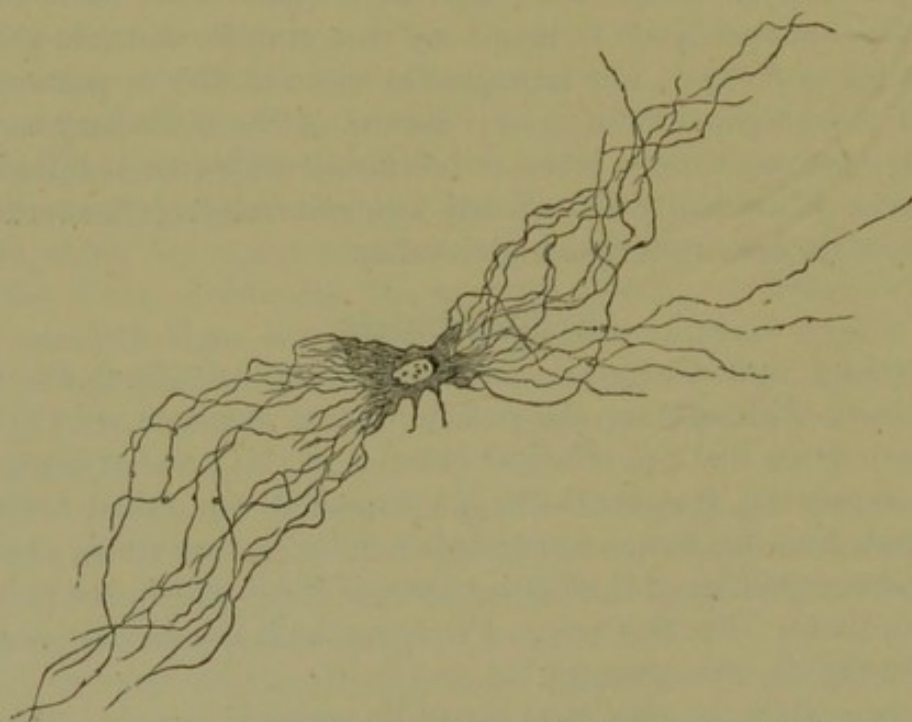


Fig. 71.—Isolated gleia-cell from the human spinal cord.  
*Magn. 800.*

for two or three days in a straw-coloured solution of bichromate of potassium or in 0.1 per cent. osmic acid. The tissue can be subsequently coloured at pleasure. It will always yield a considerable number of well-isolated gleia-cells, which vary in appearance according to the region from which the preparation has been taken.

Fig. 71 shows a cell from a radial septum of the human spinal cord. Numerous fibres of the utmost tenuity stream out from a granular nucleus which often is not very distinct. The processes, which may attain to a length of 0.5 mm., are usually disposed in two groups which run in diametrically-opposite directions. A proper cell-protoplasm is usually wanting; the cell-body is only represented by flat appendages of the nucleus, usually faintly granular, which soon resolve themselves into cell-processes, which are further distinguished by their characteristic stiffness. They hardly divide at all, whereas in other kinds of cell (nerve-cells, for example), division of the processes is very frequent. The processes of some



of the cells radiate in all directions, as, for example, in the cell shown in fig. 72, from the ependyma of the lateral ventricle (spider-cells or astrocytes). Sometimes many fine processes start from one pole of the cell and a broader, thicker process from the opposite pole, giving the appearance of a paint-brush with its handle (paint-brush cells). *Ranvier*, *Weigert*, and many others suppose that these processes of the gleia-cells (at all events when fully developed) are only fixed on to the cell-body, not actually united with it.

It is cells of this latter kind which, when prepared by *Boll's* method, are pointed out as Deiters' cells.

*Kölliker* makes a distinction between cells with very long processes ('Langstrahler') and those of which the processes are shorter ('Kurz-

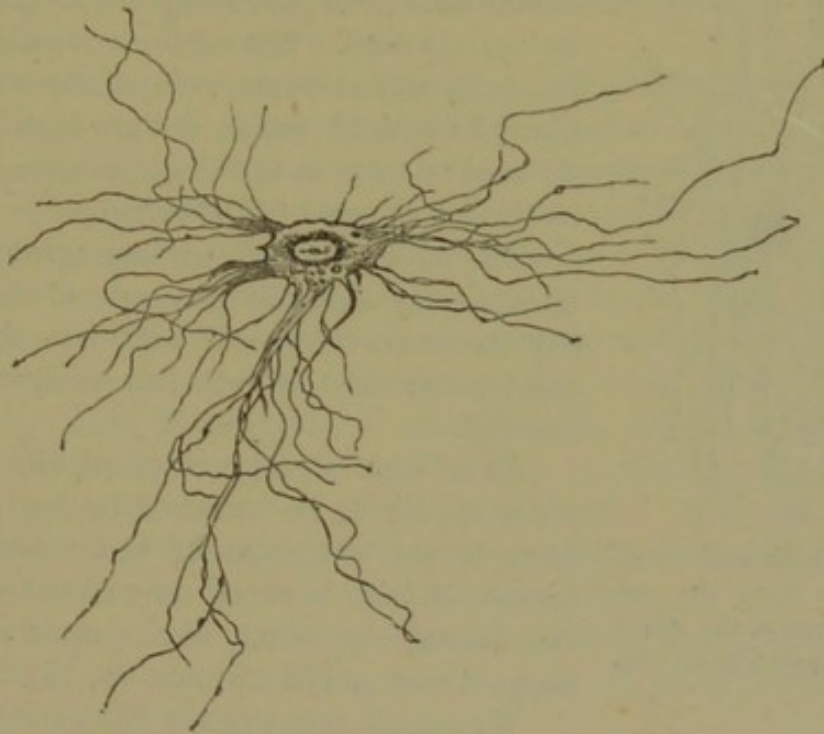


Fig. 72.—Isolated gleia-cell from the ependyma of the lateral ventricle.  
*Magn.* 800.

strahler'). The latter are found chiefly in the grey matter. *Andriezen* describes some gleia-cells with rough processes, shorter, thicker, and more branching, which are, perhaps, identical with these. He, however, looks upon them as mesodermal structures.

In many of these supporting cells of the central nervous system no nucleus is visible; it seems to be converted into chitin. In others the protoplasm is so scanty that the processes appear to start from the nucleus itself.

The disposition of the cell-processes varies according to the locality. Thin sections yield the best results, but the fine network is very difficult to pick out, with most staining methods, from the other histological elements. After staining with alum-hæmatoxylin, which gives to the nuclei an intense blue colour, their arrangement is easily grasped, but, as far as the processes are concerned, more is usually seen in carmine preparations, and this not infrequently in sections which seem from other points of view



hardly successful. Golgi's sublimate method sometimes affords pictures of the most surprising distinctness (fig. 73).

The gleial elements, though not the nervous, are said to stain particularly well by the following method:—

A perfectly fresh piece of tissue is cut into sections not more than  $1\frac{1}{2}$  mm. thick at most, and placed for from fifteen to twenty minutes in a mixture of equal parts warm water and concentrated solution of picric acid. The sections are then transferred to a hardening fluid consisting of 100 parts concentrated watery solution of bichromate of potassium and 16 parts of 2 per cent. solution of perosmic acid. This mixture should have been previously exposed to sunlight for several days. The sections remain in it in the dark, and at a temperature above  $25^{\circ}$  C., for about forty-eight hours, and are then placed for six days or more in the silver solution. Further treatment as usual (*H. Berkley*).



Fig. 73. — Gleia-cells and gleia-fibres from the anterior column of the spinal cord. Longitudinal section.

The silver method of impregnation shows most clearly that the processes of the cell do not anastomose, but end with free tips. Such anastomosis has nevertheless been repeatedly asserted.

As I have already observed, the gleia-cells often appear to be attached by one process or more to the adventitia of the vessels. As a matter of fact, however, they do not unite with the vessels, but merely form a membrane round about it (see p. 173 and figs. 78, 79).

We cannot here explain the extent to which one is justified in supposing that the gleial cells and their processes share in the lymph-supply within the brain.

In many spider cells the process (or processes, for there are often several) leading to the perivascular space differs in a marked degree from the rest. It is coarser, thicker, and often more twisted. *Bevan Lewis* gives it the distinctive name of 'vascular process.' In many other gleia-cells one or more processes are distinguished from the others by peculiarities of shape, size, etc.

The whole central nervous system is permeated and supported by a fine scaffolding, of which the cells constitute the nodal points. This is the stroma in which the nervous elements and their vessels are disposed.

Manifold local peculiarities are presented in the finer details of arrangement of this supporting tissue. In many parts (the interior of the white substance of the spinal cord, for example) the majority of the gleia-fibres, and the longest, run in the same direction as the nerve-fibres (fig. 73), while in the outer layers of the cortex, on the contrary, they generally take the opposite course towards the periphery.



On the strength of the appearances which result from his new staining method, *Weigert* supposes the neurogleia to consist of innumerable fine fibres which traverse the central nervous system in various directions, crossing one another again and again. Often a cell-platelet lies at the point where they cross, but does not unite with the fibres, the gleia-cell being merely imposed upon the gleia-fibres.

Neither the amount nor the disposition of the supporting tissue can always be brought into accordance with the theory that its sole function is to connect and support. This circumstance seems to indicate that these constituents may have another and not unimportant part to play; in connection, we may suppose, with the processes of nutrition.

*Spina* and *Vejnar* observed movements of the gleia-network and continual changes of the reticular marking in the living brain of the frog and triton after removal from the animal.

On this assumption of the capacity of movement in the gleia-fibres *Ramón y Cajal* bases the most far-reaching hypotheses with regard to the functional meaning of the gleia-cells. He supposes that the retraction of the fibres which extend to the vessels may cause enlargement of the lumen and consequent hyperæmia. To the gleia-cells of the grey substance he ascribes the power of so extending their processes as to thrust them between the arborescent system of one neuron and the cell of another, thus interrupting the contact necessary for the physiological transference of impulses. This he supposes to take place in sleep, among other conditions; but he holds that the whole function of thought is directed and regulated by the movements of these 'pseudopodia.' Here, again, I would warn the student to be on his guard against seeking to explain the higher psychical processes by details of anatomical structure.

It has already been explained that the gleia-tissue, like the nervous constituents of the central nervous system, owes its origin to the epithelial lining of the central cavities.

**Pathological Changes in the Gleial Tissue of the Central Nervous System.**—It is obvious that our altered conceptions of the central supporting tissue must modify our ideas concerning the pathological changes to which it is liable.

Hyperplasia, proliferation of the gleia-tissue in the form of circumscribed tumours, is known as **glioma**, while more diffused proliferation is usually called **gliosis** or **gliomatosis**. In either case we have unquestionably to do with an increase of the gleial elements. Gliosis of the spinal cord is associated with a tendency to decay and the formation of cavities (syringo-myelia). We have as yet no certain knowledge of how this increase of the gleial elements comes to pass. Direct division seems to play but a small part in it. *Von Lenhossék* thinks that there may be agenetic cells in the central nervous system, which normally remain throughout life in their original smooth condition, although they can be excited to proliferation by some unknown form of irritation.

True primary sclerosis of the central nervous system must be looked upon as an inflammatory process. The earlier stages are always marked



by an increase of nuclei, material for which is afforded by the lymph-cells which wander out of the vessels. Whether these lymph-cells are capable of further change, whether they can give off processes and take part in the formation of the sclerosed tissue by which the nerve-substance is compressed and finally destroyed, is a question that must be left undecided for the present. We may assume that a similar process takes place in the cortex of the brain in dementia paralytica.

In secondary degeneration (tabes, or spots of disseminated sclerosis, for example) the process is reversed; the nerve-tissue decays first, and proliferation of the supporting tissue ensues to fill the void thus created. In this case, however, the elements increase, not in number, but in size. The investigations of *Robertson* go to prove that the gleia-cells swell at first in both primary and secondary sclerosis, and this hypertrophy is the inception of proliferation. The daughter-cells also swell at first, and may themselves subdivide. New processes grow out of the cell-protoplasm; they resemble dendrites at first, but at a later stage they divide almost close upon the nucleus. The proliferation of gleia-fibrillæ takes place by preference in the direction of least resistance (*Eurich*).

Most pathological processes in the central nervous system affect the gleia-tissue.

In many cases of sclerosis the number of fibrils which originate in a single cell is greatly increased. Nuclei are seen from which innumerable delicate fibres, usually short, spread out in every direction (fig. 74). The sclerosed tissue then breaks up almost throughout into a number of spherical bodies.

Under the influence of continuous pressure, due, for instance, to the proximity of a tumour or a hæmorrhage, the gleia-cells swell and assume a turgid, glassy look; their nuclei disappear; the refraction of the processes is changed, so that, like the cells, they become more distinct; sometimes the gleia-cells come to resemble nerve-cells; in the neighbourhood of a hæmorrhage they are apt to imbibe a little blood-

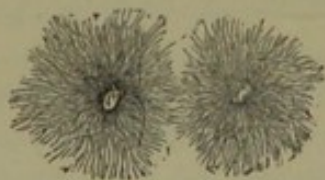


Fig. 74.—Gleia-cells with numerous short processes from the corpora quadrigemina which were affected with sclerosis in a case of dementia paralytica. *Magn.* 250.

pigment. These are the changes which characterise inflammatory swelling of the gleia-cells. Proliferation of nuclei by karyokinesis (*Coën*, *Fürstner*, and *Knoblauch*) also occurs; some cells occasionally taking on the form of irregular plaques containing as many as twelve to fifteen nuclei (fibroplastic bodies of *Hayem*).

The granulation of the ependyma of the ventricle so commonly observed depends upon an overgrowth of the subepithelial supporting tissue which, breaking through the epithelium, appears uncovered in the ventricular cavity. In old brains, especially, a yellowish-brown pigment is often found in the gleia-cells.

Changes, of which varicose swelling of the processes is the commonest, can be observed by means of the silver method in alcoholic poisoning



(*Berkley*), uræmia (*Sacerdotti* and *Ottolenghi*), dementia paralytica (*Mills* and *Schirely*), and other conditions.

This granulation usually gives the surface of the ventricle a gravelly appearance, though it sometimes forms nodules as large as a grain of millet seed. It is occasionally found in the brains of healthy persons of advanced age; but it almost invariably points to chronic brain trouble, and is met with most frequently in dementia paralytica. The granulations may occur in any part of the ventricles, but are apt to be most noticeable in the posterior part of the fourth ventricle and over the corpus striatum.

## B. TISSUES OF MESOBLASTIC ORIGIN.

### I. CONNECTIVE TISSUE.

In the section upon neurogleia (p. 165) we have already gone into the question as to whether, and how far, we are justified in assuming that any true connective tissue bears a part in forming the scaffolding of the central nervous system. A circumstance which deserves special mention is that in this system the true connective tissue and the actual nerve-substance are always separated by a sheet of gleia-substance. It seems not impossible that mesoblastic tissue may appear in the central nervous system, either in certain pathological conditions, or in the form of tumours (such as sarcoma), or, perhaps, as a cyst-wall in the formation of sclerotic cicatrices. But in this matter, as in others, we must await the results of more exhaustive study.

### 2. VESSELS.

The structure of the blood-vessels of the interior of the brain is best studied by means of pieces not inconveniently small (the size of a cob-nut or larger), which have been macerated for one to two days in a very weak light-yellow solution of bichromate of potassium—it is well to put aside for examination a piece of cortex with medullary centre, and of the basal ganglia; the vessels can without difficulty be detached with needles from the surrounding substance under water. Fairly large vessels with all their ramifications may thus be removed.

The vessel is now examined in a drop of distilled water or very dilute glycerin. It is undesirable to use pure glycerin or strong salt solution on account of the shrivelling of the coats of the vessels and consequent confusion which is induced. The vessel can be laid whole in picrocarmine or any other stain—in a watery solution of Bismarck-brown (1 in 300), for example (*Löwenfeld*)—and examined in water after a thorough washing. The nuclear structures of the vessel are clearly shown in this way. Such water preparations can be preserved for years unchanged by surrounding the cover-slip, after its margin has been allowed to dry, with dammar varnish. Preparations in weak glycerin last better than those in water



only. For certain details of structure, normally or pathologically present, the vessels must be studied in section, after hardening.

Certain peculiarities of structure distinguish the blood-vessels of the interior of the central nervous system from all others. This is especially true with regard to the arrangement of the tunica adventitia. On account of these peculiarities it is worth while to describe separately the arteries, veins, and capillaries.

Genuine lymphatic vessels are not found in the brain or spinal cord. The lymph-paths can be shown to be clefts between the tissue-elements. Adventitial and perivascular lymphatic tracts surround the vessels, and the nerve-cells lie in lymph-spaces.

(a.) **Arteries.**—Four layers may be distinguished in the coats of all arteries of the brain-substance, except the smallest. From within outwards they are named—endothelium, membrana fenestrata, tunica muscularis, and tunica adventitia. The space in which the blood-vessel lies is lined by a delicate limiting membrane which adheres closely to the brain-substance after the vessel is pulled out.

**Endothelium** (fig. 75, a) is a delicate membrane formed by the apposition of elongated cells, the outlines of which are brought out by the silver method of impregnation. The nuclei of endothelial cells are oval or hone-shaped, with their long axes arranged in the direction of the vessel. Lying on the nucleus, or, in some cases, partly in its interior, is often seen a minute, strongly-refracting granule of unknown meaning.

If in preparing the vessel the endothelium has been dragged upon, it is apt to happen that clefts in the delicate endothelial coat are produced, which have the appearance of the nuclei of fusiform cells with elongated processes.

**Membrana fenestrata** (fig. 75, b), which lies next to the endothelium, but does not adhere tightly to it, is a coarse elastic membrane with a great tendency to arrange itself in longitudinal plaits. In transverse sections it shows as a bright undulating band. It contains neither nuclei nor other cellular elements. When strongly magnified it presents numerous clear points (? holes). This membrane it is which lends to the larger arteries, in which it should be specially studied, their look of longitudinal striation. Its existence is still to be proved in the smaller arteries, for it rapidly dwindles in importance with their diminishing calibre. It is not present in the smallest vessels or in capillaries.

Spindle-shaped plain muscle-fibres closely invest the membrana fenestrata, composing the **tunica muscularis seu media** (fig. 75, c). Without exception these muscle-fibres are disposed around the vessel with their axes, and hence with their fusiform nuclei at right angles to it. The nuclei of the endothelium and of the muscle-fibres, therefore, cross one another at right angles (figs. 75 and 76). The muscle-wall appears on its outer side distinctly ribbed, owing to the elevation of its fibres. While in the larger vessels the muscular coat is many-layered and constitutes the chief thickness of the vessel-wall, it consists in small arteries of but a



single sheet. As the vessels diminish in calibre the muscle-cells change in shape, becoming progressively shorter and broader. Their nuclei change in the same sense. A single muscle-fibre is long enough to make more than one circuit round a small vessel.

In very large cerebral arteries longitudinal bundles of connective tissue are sometimes to be observed on the outer side of the muscular coat. Usually the muscular coat stands free in a space bounded on the outside by the **adventitial coat**, or, shortly, **adventitia** (figs. 75, *d*, and 76). If it is isolated from the other coats it appears as a delicate sheet of connective tissue sown with round or oval nuclei. On the periphery of these nuclei a distinct protoplasmic granulation is often visible. Many observers have

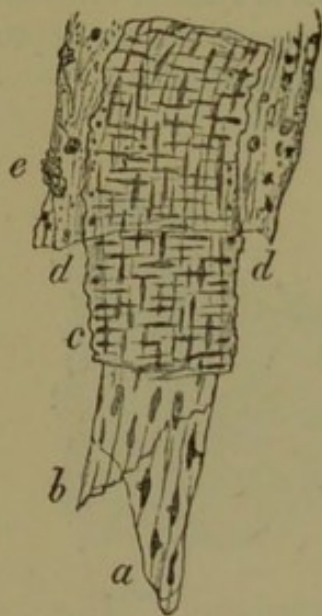


Fig. 75.—A middle-sized artery of the brain so torn as to expose each of its coats separately for a certain distance. *Magn.* 300.—*a*, Endothelium; *b*, membrana fenestrata; *c*, tunica muscularis; *d*, adventitia; *e*, pigment.



Fig. 76.—A small artery from the brain. Several clumps of pigment on the adventitia. *Magn.* 150.

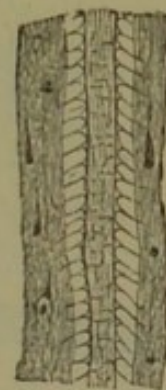


Fig. 77.—An artery from the cortex cerebri in longitudinal section. *Magn.* 80. Numbers of fine fibres are seen streaming into the brain-substance.

shown, by treatment with silver nitrate, endothelial cells both on the inside and the outside of the adventitia. Granules of pigment are invariably found in the adventitial sheath (figs. 75, *e*, and 76). More rarely fat-granules also are present (fig. 81). We shall speak of these later on.

In sections of hardened brains, especially of animals, strong fibres of varying length are often seen traversing the nerve-substance to fix themselves with conical bases to the outside of blood-vessels. Not rarely such a fibril can be followed, in the opposite direction, to a stellate glia-cell (fig. 78). Since the adventitia in the hardened preparation lies close to the muscularis, and even in the most carefully-isolated vessels no such processes are to be seen hanging on to the adventitia, it is necessary to suppose that the tube of brain-substance in which the adventitia lies is



lined with a **limiting membrane** intimately connected with it and belonging to the neurogleia. Sometimes in sections which otherwise are hardly successful, one sees a great number of these prolongations very regularly arranged (fig. 77).

The most detailed account of this limiting membrane is that given by *Lloyd Andriezen*. He states that three kinds of connective-tissue cells go to form it. In the membrane itself are found cells (fig. 79, 1) of which the processes, arranged transversely, line the perivascular space, and cells (2), of which the processes run longitudinally along the course of the vessel. There are found, besides, the oft-mentioned processes of remoter cells (3); so that the membrane must be looked upon as a felt-work of connective-tissue fibres. Round the larger vessels it is often of considerable thickness. Its physiological meaning (at least in part) may be to protect the brain-substance from the pressure of hyperæmic vessels.

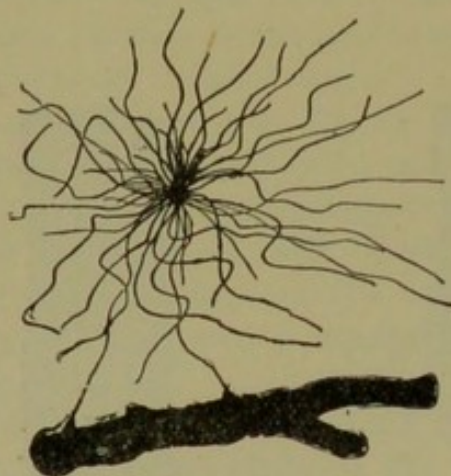


Fig. 78.—Glia - cell from the medullary substance of the great brain, from which two processes pass to a blood-vessel. *Silver prep.*

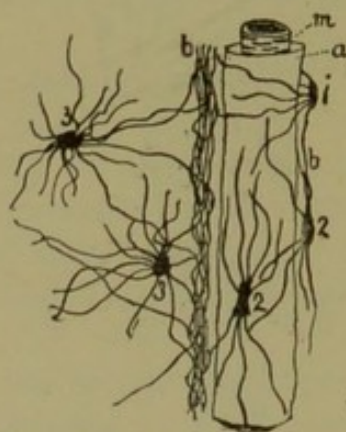


Fig. 79.—Semi-diagrammatic representation of the formation of the limiting membrane, made by the help of *Andriezen's* illustrations. *a*, Adventitia; *b*, limiting membrane; *m*, muscularis; 1, glia-cells with circular fibres lying in the limiting membrane; 2, similar cells with longitudinal fibres; 3, remoter glia-cells.

Between the adventitia and the muscularis a considerable space is seen in all isolated arteries, the adventitial lymph-space (Virchow-Robin space). The outside of the adventitia between it and the limiting membrane is also surrounded by a space, the perivascular space, or space of His. By lymph-space is meant in this sense any lymph-filled gap which may serve as the starting-point of lymph-vessels. The lymph-spaces, especially the perivascular ones, serve for the rapid exchange of juices between the plasma and the several nervous elements, in which the glial cells affixed to them probably play an important part. In very favourable injection-preparations from the new-born child one can convince oneself that tissue-spaces are injected which connect the perivascular space with the space by which every cell is surrounded (the pericellular spaces). The



pericellular spaces are visible in very thin sections, and occasionally their connections with perivascular spaces may be seen (fig. 80). A slender crescent-shaped body is sometimes found squeezed against the outer wall of the pericellular space. *Friedmann* looks upon it as the nucleus of an endothelial lining cell. According to *Paladino*, a fine network starting from the supporting tissue of the grey substance, traverses the pericellular space to fix itself on to the nerve-cell. There may be some confusion here with the nerve-endings described on p. 156. To exhibit this extremely fine network, small pieces of spinal cord, hardened in chrome-salts, are placed for several days in a solution (1 in 1000) of palladium chloride weakly acidified with hydrochloric acid, and then transferred to a 4 per cent. watery solution of iodide of potassium, in which they must remain for twenty-four hours at least. Dehydrate in alcohol and embed in paraffin. Even though we allow that in the hardening process the pericellular and perivascular spaces are increased in size, owing to the shrinking of the

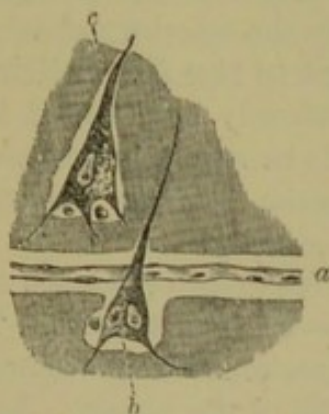


Fig. 80.—Section from the cornu Ammonis, showing perivascular and pericellular lymph-spaces. Stained with carmine. Magn. 150.—a, Capillary vessel in a perivascular lymph-space; b, pericellular lymph-space directly continuous with the former. Two leucocytes are seen in the pericellular space c, and one in the space b.



Fig. 81.—A small vein from the brain-substance. Magn. 150.—a, A clump of fat-granules on a small lateral branch; b, an indistinctly fusiform enlargement.

tissues, the normal existence of such spaces is proved by the presence within them, especially about the larger cells, of one or more free round cells. The lymphatic nature of these has been denied by some observers; *Andriezen* professes to distinguish short processes attached to them, but cannot define precisely the meaning of the cells. It is probable that during the increase and decrease in size of the brain the lumina of the canals lined by the limiting membranes are subject to numerous fluctuations even under normal conditions. Within these canals the complementary relations as to area of cross-section of the lumen of the vessel, and the adventitial and perivascular spaces, is perpetually varying. An increase in the lumen of the artery can only occur at the expense of one or both of the lymph-spaces.

(b.) **Veins.**—Only three coats can be recognised. The endothelium



(fig. 81) is distinguished from that of the arteries by the rounder form and less regular arrangement of the nuclei.

The second layer, which forms the proper vessel-wall, consists, except for scattered plain muscle-fibres found especially in the larger veins, only of connective-tissue structures with numerous irregularly-scattered nuclei.

The adventitial lymphatic coat is a delicate membrane, essentially similar to that already described for the arteries. The points in which it differs will be noted later on. It may be assumed that the channels in the brain-substance occupied by the veins are lined by a limiting membrane.

(c.) **Capillaries** (fig. 82).—Capillaries may be regarded as the continuation across from arteries to veins of the endothelial coat of the vessels,



Fig. 82. — Isolated capillaries from the cerebral cortex. *Magn.* 100.

for they consist of this coat only with a closely-adherent adventitial sheath. The endothelial coat has acquired, from the necessities of its independent position, a greater strength than it possesses in the arteries and veins.

(d.) **Fat and Pigment in the Adventitia of the Brain-Vessels.**—It has already been stated that pigment and fat-granules are to be regularly met with in the adventitia of the small vessels. A fuller explanation of the normal appearance is necessary.

Numerous cells filled with drops of fat are scattered throughout the brain of the new-born child—fat granule-cells. They are supposed to supply the material for myelin formation. Such fat granule-cells are found hanging on to the adventitial sheath of the vessels. A layer of fat is seen covering the adventitia in children in the first few years of life. After the fifth year some of the fat-granules, especially about the arteries, are always found to have assumed a distinct yellow colour, being changed into pigment. In the brains of adults the presence of cells containing yellow or yellow-brown granules may be looked for with confidence in the adventitia of the arteries. The cells present every gradation of granules; in some they are small and irregular, in others numerous and large. Many reagents, concentrated sulphuric acid for instance, fail to affect this pigment. Osmic acid gives it, especially when the pigment is light in colour, a shade of grey.

It is quite otherwise with the adventitia of the veins. Pigment is only present in small quantities. Fat surrounds the veins in every brain examined. It may be scattered irregularly over the adventitia in the form of small drops. Fat granule-cells are, on the other hand, often met with, looking under a low power like dark spots on the vessels. Fat-granules and fat granule-cells are sometimes scattered over the adventitia (fig. 81); sometimes they form a ring around the vessel, giving to it a fallacious appearance of fusiform enlargement.

It must be granted that the fat in the adventitia is a remnant of the embryonal period; later, it undergoes, especially in the region where metabolism is most active, a chemical change into pigment, probably by



oxidation. The pigment is not, therefore, a degeneration-product of blood-pigment which has transuded from the vessels. In all its chemical characters it differs from blood-pigment, and is to be, equally with the fat, looked upon as a normal appearance. The oxidation of fat into pigment occurs to a less extent around the veins, owing to the small amount of oxygen which the blood in these contains.

(e.) **Pathological changes in the small Brain-Vessels.**—In considering changes in the vessels it is necessary in the first place to determine which coat of the vessel is diseased, for the process is quite different in the several coats. Disease of the adventitia contrasts, for example, with disease of the muscularis.

It is worthy of remark, too, that one often meets with alterations of the vessel-walls of the brain which have given rise to no symptoms during life, but which yet are distinctly pathological in their nature even if they are not serious enough noticeably to affect the nutrition of the brain.

Granular pigment, which might easily be mistaken for normal blood-pigment, is found in the brain as a residuum of hæmorrhages, and perhaps



Fig. 83.—Cells with hæmatoidin crystals from the walls of an old apoplectic clot. *Magn.* 200.



Fig. 84.—A moderate-sized artery from the corpora striata, with numerous pigment-cells in its adventitia. *Magn.* 80.



Fig. 85.—Capillary vessel from a case of melanæmia. *Magn.* 200.

also as the consequence of prolonged hyperæmia. **Hæmatoidin** (the name given to this pigment) differs from normal blood-pigment in certain unmistakable respects. In colour it is a browner red, and it shows a tendency to crystallise in rhombic prisms, which may be found in the fat-granule cells, sometimes several together (fig. 83). A similar pigment derived from the blood is, as a rule, found in the surrounding brain-substance. If the characters are not sufficient to differentiate the pigment, its chemical behaviour affords an unmistakable test. On addition of concentrated sulphuric (or other mineral) acid the pigment passes through a series of colour changes, becoming green, blue, violet, and, finally, dissolving. This reaction can easily be obtained with any piece as large as a millet seed from the contents of an old hæmorrhagic cyst. Even after the brain has been hardened in chromic acid, a very small piece placed on a



slide and allowed to dry affords this play of colours on addition of the acid. The blue-green spots are visible to the naked eye.

A peculiar pigmentation is sometimes met with in the adventitia of the vessels which enter at the base of the brain. Elongated cells, with thick knotty processes, are quite filled with dark-brown pigment. The nucleus alone appears light, as if it were a space punched out of the cell (fig. 84). Besides these, many round **pigment cells** are seen scattered singly or united into chains. Such cells occur normally in the pia mater, especially on the ventral surface of the medulla oblongata. No pathological importance, therefore, attaches to them. They have simply been drawn up along the course of the vessels from the meninges into the substance of the brain.

A fourth kind of pigment is to be mentioned, having its origin in the blood, and, therefore, not belonging to the adventitia, although occasionally fixing itself in it. This pigment, **melanin**, occurs in the brains of people who have suffered from violent epilepsy (fig. 85). It appears as very fine black granules, which are contained in the red blood-corpuscles, seldom adhering to the walls of the vessels and very rarely occurring on the outside, and gives to the brain-substance a striking grey colour. This pigment also offers great resistance to chemical reagents. It is easily seen that the blood-corpuscles carry these pigment-granules, for large granules are found in emboli which have led eventually to rupture of the vessel.

**Collections of fat** in the adventitia may also attain to pathological importance, as, for instance, in cases of softening of the brain and spinal cord. It is not possible to place a limit upon the amount to which accumulation of fat-granules in the adventitia may attain in health. In disease the quantity becomes so great that the vessels appear to the naked eye as thick yellowish-white columns.

**Fatty degeneration of the muscular coat** presents essentially different features (fig. 86). In the earliest stage of this condition bright shining fat-drops appear between the muscular fibres of the arteries. Later on the fat-granules fill the muscle-fibres themselves, which become dull in appearance, their nuclei lose their distinctness, and the muscle-coat constitutes simply a dim yellowish tube invested by the adventitia. Although such arteries with fattily degenerated media must have lost considerably in resistance and elasticity, they may be found in quite healthy brains, even of young people. It must be unconditionally accepted, however, that such a condition gives a tendency to rupture of the vessels, and consequent hæmorrhage.

**Calcification** of the vessels is not rare. It occurs under different forms. Simple calcification of the media (fig. 87), is to be met with in healthy persons, even children. Calcification may occur in patches, or the whole artery may be converted into a tube of chalk invested by its adventitia. Examined macroscopically, the vessels look like white threads. They grate when pressed upon with a needle. Angular fragments of these calcified tubes are seen in sections. To make quite sure of their nature, a drop of sulphuric acid is allowed to run in under the cover-slip,



when bubbles of carbonic acid gas escape, and crystals of sulphate of lime make their appearance.

The second form of calcification of vessels has a more important pathological significance. It begins in the adventitia, but soon extends beyond the limits of this coat, bulging into the brain-substance as rounded, knotty, chalky structures (fig. 88). The more advanced phases of this process are only found as concomitants of other diseases of the brain.

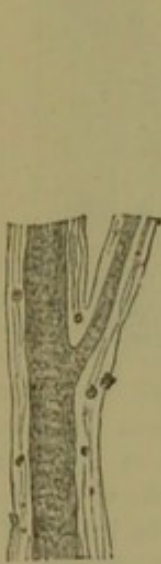


Fig. 86.—Fatty degeneration of the muscular coat of a cerebral artery. *Magn.* 150.

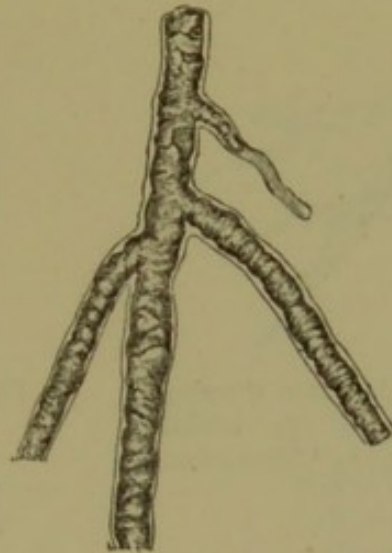


Fig. 87.—Calcification of the muscular coat of a vessel of the brain. *Magn.* 150.



Fig. 88.—Calcification of an artery of the brain affecting the adventitia as well as its other coats. *Magn.* 150.

Calcification of the capillary network is sometimes met with in circumscribed regions; in the globus pallidus (*Wollenberg*) and the nuclear layer of the cerebellum, for instance.

Connective-tissue overgrowths originating in the media affect especially the veins. At first the lumen of the vessel is not altered, while its circumference is increased; therefore the endothelium as well as the adventitia remain intact. **Fusiform hypertrophy** of the vessels of the brain is thus produced (figs. 81 and 89), especially at the spots where the brain-vessels give off numerous fine branches, almost at a right angle, as, for example, the vessels going into the brain from the great veins at its base or the finest branches of the meningeal arteries which are destined for the surface of the cortex (*Neelsen*). As the process advances the lumen of the vessel is diminished, even to obliteration. The adventitia is drawn into the process. The part of the vessel in front of the overgrowth, now put out of function, dwindles to a connective-tissue thread (fig. 89). This kind of obliteration of the vessels is commonest in the veins, and especially in the veins of old atrophied brains. After the fiftieth year it can also be found in almost every case in the arteries. Even in children's brains it is not invariably absent.



Very extensive connective-tissue hypertrophy of the vessel-wall, often accompanied, however, by considerable enlargement of the lumen of the vessel, is met with in places where the nervous tissue is sclerosed. It occurs also as the result of irritation—the inflammation which surrounds tumours, for example.

In the brains of animals affected with rabies, *Golgi* found frequent karyokinesis of the nuclei of the muscle-fibres of the vessel-wall; in a small

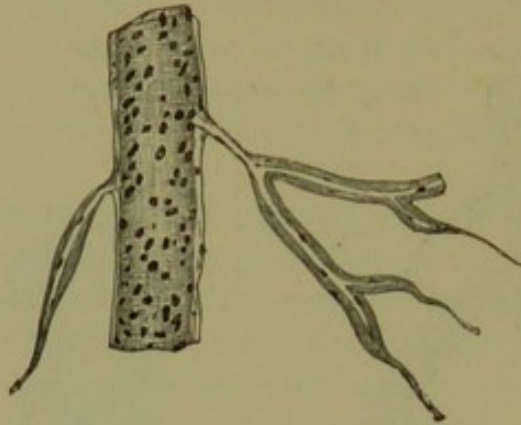


Fig. 89. — A vein from the brain showing fusiform hypertrophy of its lateral venules resulting in their obliteration. *Magn.* 150.



Fig. 91. — Atheromatous degeneration of the tunica intima of an artery of the brain. The dark patches of atheroma are seen to reach no farther than the muscular coat, which appears as a bright crenulated seam sharply marked off, both from the lumen and the surface of the tube, differing in this respect from fig. 75. *Magn.* 150.



Fig. 90. — Pseudo-hypertrophy of the muscular coat of an artery of the brain. *Magn.* 150.

number of cases he could, in addition, see such division-figures also in the connective-tissue epithelium and nerve-cells throughout the whole nervous system.

A form of degeneration of the muscular coat, especially important in connection with hæmorrhages, is the condition known as **pseudo-hypertrophy** (granular degeneration). In groups of muscle-fibres fine roundish granules make their appearance; the granulation increases, the fibres fuse together, and so an opaque, usually wedge-shaped mass is formed, the rounded base of the wedge projecting somewhat beyond the general periphery of the media (fig. 90). A granular disintegration of the muscularis supervenes for a longer or shorter extent of the vessel-wall (*Löwenfeld*).



**Fatty atheroma of the intima** is recognised, as a rule, by the dark granular patches on the inside of the vessel, the subjacent muscularis remaining unchanged (fig. 91). If a teased vessel mounted in glycerin is under examination, it is often possible to loosen some of these atheromatous patches by pressing on the cover-slip; the detached piece floats about freely within the tube until it gets wedged, as a rule at the point of junc-



Fig. 92.—Beaded enlargement of a large artery of the brain. *Magn. 50.*

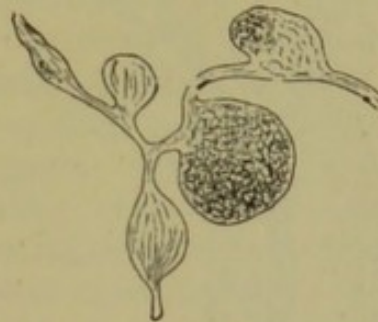


Fig. 93.—Miliary aneurysm of very small vessels. The dilatations are partly filled with blood. *Magn. 50.*

tion of two branches. This gives us an idea of the process by which an embolus is formed in a small artery. When more strongly magnified it shows an amorphous mass containing shining fat-granules. In many cases of apoplexy such atheromatous degeneration is visible in the arteries, and hence it is possibly not an unusual condition, especially in old brains.

**Colloid degeneration** is a not uncommon condition of the vessels of

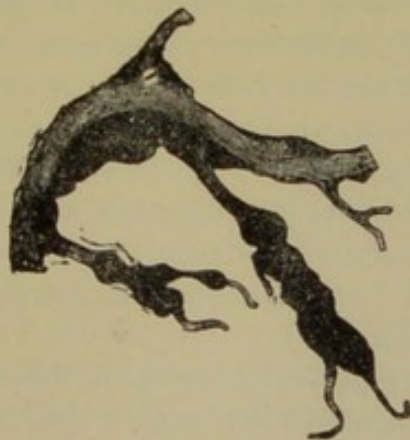


Fig. 94.—Aneurysmata dissecantia from the neighbourhood of an apoplectic lesion. *Magn. 50.*

the spinal cord; their walls are converted into a shining hyaline mass, taking a deep colour with carmine. More than one condition distinguished by special chemical reactions is included under the name of colloid degeneration.



There is also a *hyaline degeneration* of the brain-vessels, in which the substance termed 'hyaline' soaks through the vascular wall and clings to its outer surface in fairly even drops.

**Aneurysm** of the brain-vessels, especially localised aneurysm, occurs in various forms. Paralytic dilatations of the small arteries are to be seen in the brains of chronic lunatics (fig. 92); a striking irregularity in the calibre



Fig. 95.—Ampullar dilatation of the adventitial lymph-space surrounding an artery of the brain.  
*Magn. 50.*



Fig. 96.—Packing of an adventitial lymph-space with leucocytes.  
*Magn. 100.*

of the vessels characterises them. The muscularis exhibits a series of bead-like dilatations separated by constrictions. They are caused by deficient innervation of the vessel-wall—a condition of partial paralysis, or by sclerosis of the artery. A higher form of the condition constitutes **miliary aneurysm**, which, however, may also arise in other ways (*Löwenfeld*). Larger and smaller aneurysmal dilatations are especially common in the neighbourhood of apoplectic lesions; but it would be a mistake to suppose that all hæmorrhages are due to the rupture of such dilated vessels (fig. 93). The small aneurysms are often due simply to the swelling of the adventitial sheath from the unequal distribution of the extravasated blood within it (*aneurysmata dissecantia*, fig. 94).

Miliary aneurysms are generally found in the small arteries and capillaries. They are more numerous the smaller they are. For the most part they are globular or fusiform, and situate on the side of the vessel, with which they are sometimes connected by a stalk. They are very rare in the vessels of the spinal cord (*Borgherini, Hebold*).

The **adventitia** may also be **hypertrophied** in certain situations; sacciform dilatations of the vessels are thus formed in otherwise healthy brains. When they reach a certain size they make conspicuous spots in the



brain-tissue, which are to be looked upon as **lymph-cysts** (fig. 95). When these dilatations of the adventitia are large and freely scattered throughout the brain-substance a sieve-like appearance is produced, the *état criblé*, as it has been termed, which is sometimes to be seen in the brains of old people. Spaces exactly similar in appearance are produced when by shrinking of the nervous tissue the perivascular spaces are dragged upon and enlarged. The very similar appearance sometimes produced by changes in the myelin-sheath of large nerve-fibres (*Vassale*) must not be confounded with the true *état criblé*.

Cystic formations are commonest in the grey, sieve-like degenerations in the white substance.

The formation of new vessels has frequently been described, chiefly in relation to the substance of the cortex. As, however, there is no space prepared for the reception of such comparatively large objects as vessels, an overgrowth by proliferation from the existing vessels could only take place at the expense of other tissue elements. In many of the cases described there is certainly no new formation; what happens is that capillary loops, which in ordinary circumstances might easily be overlooked, are more distended with blood and therefore show more distinctly.

The **contents of the adventitial lymph-spaces** deserve especial consideration.

When the cover-slip is made to press upon and so spread out the adventitia its spaces are seen to contain certain formed elements, amongst which lymph-corpuscles are the chief. Besides these, drops of fat, pigment-granules, vesicular cells of very large size (altered leucocytes, perhaps), and even blood-corpuscles, are also seen within this space. The presence of many red blood-corpuscles suggests aneurysma dissecans, a rupture of the inner coat rather than pure diapedesis.

The quantity of leucocytes within the adventitial lymph-space may be so great that the muscular coat appears to have a distinct covering of them. This condition (which has been mistaken for nuclear proliferation, but is, in fact, due to increased emigration of white blood-corpuscles) is met with in inflamed and hyperæmic conditions of the brain and also in progressive paralysis (fig. 96).

The elements already described are normally present in the lymph space; but distinctly pathological products also are to be found within it. In purulent meningitis these spaces are filled for some distance down into the brain-substance with pus-corpuscles.

Of great importance is the appearance of **neoplastic** elements (sarcoma- and carcinoma-cells) in the lymph-spaces, especially in the neighbourhood of tumours. It shows that in the brain the lymph-paths are the most important tracts along which such growths extend.

In syphilis accumulations of peculiar cells are found in the adventitial lymph-spaces. The cells are large, transparent, nucleated, and not unlike the cells of embryonal tissue. Further, there are to be found in the same situations (and also within the perivascular spaces in cases of long-standing infantile paralysis [*Leyden*, *Goldscheider*] and in myelitic lesions) accumu-



lations of cells like the cells of endothelium. Endothelial cells may also be heaped up into papillose excrescences of the adventitia (*Arndt*).

In various inflammatory conditions in the spinal cord, and also in rabies, a peculiar structureless colloid mass is found to be discharged around the arteries, especially the larger ones. It stains more or less strongly with carmine; when this mass, which originates in the blood, saturates, as it may do, the arterial wall itself, it gives to it when stained a peculiar brilliance. Similar colloid effusions are sometimes to be seen around the arteries in otherwise normal cords.

Lastly, attention must be called to the fact that the **contents of the vessels** also deserve consideration. Often the blood within them remains almost unchanged. In other cases it is coagulated in a special manner, a central cord of fibrin surrounded by a network of threads filling up the vessel. The endothelial coat may be loosened and lying in the lumen. The coagulation takes, at other times, a different form without our being able to trace the influence upon it of local causes; peculiar shining globular masses of coagulum are seen lying either separately or associated in groups; but, still, they are only products of the blood-plasma.

Special attention must be called to the constituents of the emboli which block the vessels. At times (as in leukæmia) they are formed by roundish masses of white blood-corpuscles; or, again (after fractures), the emboli consist of drops of fat; or they may be formed (in epilepsy) of the peculiar pigment already mentioned, or, in still other cases, of atheromatous patches detached from the vessel-wall. Pieces of inflammatory lymph from the heart or great vessels are only exceptionally carried as far as the small intra-cerebral vessels. The elements of neoplasms which have found their way into the blood, and even bacteria, occur in the emboli of brain-vessels. One must be cautious, however, in the last case to exclude the products of post-mortem putrefaction.

Not seldom such diseases of the vessel-walls as aneurysm or calcification are limited to certain layers of the cortex of the cerebrum and cerebellum. So, too, with regard to the contents of the vessels, special forms of coagulum may distinguish particular strata of the cortex. This fact makes it appear probable that the several layers of the cortex are, up to a certain point at any rate, independent of one another in respect to the nutrition and innervation of their vascular networks.

## OTHER TISSUE-ELEMENTS WHICH OCCUR IN THE CENTRAL NERVOUS SYSTEM.

Besides those elements already described, which actually take part in building up the central nervous system, there are others which always, or almost always, put in an appearance when the nervous system is diseased, and afford by their nature and arrangement important evidence as to the character of pathological processes.

(1) **Free cells** (migratory, or lymphoid cells) indistinguishable from



leucocytes, are to be met with in all parts of the central nervous system, into which they probably migrate from the blood-vessels. In pathological conditions, inflammatory processes especially, their number may be largely increased.

(2) **Fat granule-cells**, already repeatedly noticed, are perfectly round cells with, usually, distinct nuclei, and filled out with brilliant round drops of fat (fig. 97). As a rule, they are lymphoid cells, which have either stuffed themselves with fat for the purpose of transferring it to developing medullated nerves; or else have taken into their substance, with a view to eventually carrying it away, the fat set free in the degeneration of such medullated fibres. When rapid degeneration is taking place at any spot, as in encephalitic lesions, drops of myelin are shown by Weigert's method of colouring to be present in quantities in neighbouring fat granule-cells. Whether fat granule-cells are also formed from nerve-cells and connective-tissue cells by fatty degeneration must be left, as yet, an open question. Even the plain muscular fibres of the vessels are supposed when fattily degenerated to have a similar fate (*Huguenin*).

The presence of fat granule-cells is most easily detected by squeezing a little piece of the fresh tissue under the cover-slip. They are always to be looked for when degenerations are occurring in the spinal cord as well as in embolic lesions of the brain. Under a low power they appear as distinct dark spots; an estimate as to their quantity may be made in this way. When they are very numerous, lying in heaps, yellowish white flakes and stripes, dark in transmitted light, are visible, even with the naked eye. One great advantage of Marchi's method of osmium-staining is that it enables us to distinguish fat granule-cells in sections as black globular bodies.

(3) **Amyloid bodies** are seen under the microscope as clear, strongly refracting, round or oval bodies characterised by their brilliancy when slightly magnified. Unlike the granules of vegetable starch, they do not appear to consist of concentric layers, though in the larger corpuscles a round kernel and an outer husk can be distinguished. Unlike vegetable starch again, they are not doubly-refracting. Dilute tincture of iodine stains them a light blue colour, the subsequent addition of a little sulphuric acid turns them a deep violet. The reaction is generally successful, even in sections. When stained with alum-hæmatoxylin they assume a fine blue colour. Generally speaking, they take all nuclear stains readily.

They are most numerous in later life, and are particularly common in regions in which much neurogleia is present; although even there they show a preference for some situations rather than others (*Redlich*). One may count upon finding them in the cord of persons over forty years of age, especially in the layer of grey cortex on the periphery, the largest numbers being usually collected about the point of exit of the posterior roots. Starting from the periphery, they can be seen scattered freely along

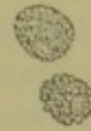


Fig. 97.—Two fat-granule cells from the spinal cord. The area in which they occurred was secondarily degenerated. *Magn.* 250.



the septa and vessels. They are thickest in the white substance of the posterior columns. Places in which they are almost invariably to be found in the brains of old persons are—the outermost layer of the cortex cerebri (*Kostjurin*), the neighbourhood of the chiasma nervus opticum, the septum pellucidum, and, last but not least important, the tractus olfactorius. Both in the spinal cord and cerebral ventricles they are frequently met with in the deepest strata of the ependyma.

Generally speaking, no pathological process seems greatly to influence the appearance of these bodies, excepting the gradual atrophying processes of which senile atrophy may be taken as the type. Large quantities of them are occasionally found in the ependyma of the cornu Ammonis when it is sclerosed in epilepsy.

No satisfactory explanation of their origin has yet been given, but by far the most likely supposition is that they develop from the nuclei of the neurogleia (*Rindfleisch* and *Redlich*). The substance of which they are composed is not really related to starch, but to albumin. It is very doubtful whether they result from chemical changes in the disintegrating nerve-fibres, but it is noteworthy that they have been identified with certainty in no organ out of the central nervous system, except, perhaps, the lungs. The so-called amyloid bodies of the prostate glands are concretions of quite another character.

*Bevan Lewis* gives the name of **colloid bodies** to round nodules very similar to the last, with a diameter of from 6 to 40  $\mu$ . They are perfectly transparent and homogeneous, stain weakly with hæmatoxylin, and are quite unaffected by carmine, aniline colours, iodine, and sulphuric acid. They are said to originate from the degeneration of nerve-fibres, and frequently appear in large quantities in the brain and spinal cord in the most divergent forms of central disease. They are almost entirely confined to the white matter or those parts of the grey which are most richly supplied with medullated fibres.

(4) The central nervous system also contains within itself the elements of the various neoplasms which have their seat there.

(5) **Leber's corpuscles** are strongly refracting transparent globular bodies, about as large as the nuclei of the largest nerve-cells, which appear to be formed in the inside of the non-medullated nerves to which they are found attached. They are described under this name by *Vincenti*. They are supposed to be essentially different from amyloid bodies in chemical constitution, and are found especially where nerve-substance is affected by a tumour.

(6) Various **bacteria**, as, for example, the bacilli of typhus and splenic fevers (*Curschmann*), migrate into the central nervous system, where their presence may be revealed either by the microscope or by cultural experiments. By agglomeration in the finer blood-vessels they may even give rise to embolism (*cf.* p. 184).



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## SECTION IV.—MINUTE STRUCTURE OF THE SPINAL CORD.

### STRUCTURAL FEATURES COMMON TO ALL THE CENTRAL ORGANS.

THE gross anatomical features in the structure of the central nervous system, as seen with the naked eye, have received due attention in the second section. We must now prepare ourselves to appreciate the physiological meaning of the several organs by carefully studying their anatomical connections; this is the task of minute anatomy, a most difficult task, and still far from receiving its solution.

Certain general considerations which will aid us in the solution of other problems, as well as in dealing with the spinal cord and the brain, must first be set forth; the subsequent explanation of details will be thereby facilitated. The more our knowledge of the minute structure of the central organs widens, the more possible does it become to present to the reader an exact and detailed "general anatomy of the central nervous system." It is a difficult task to deduce from the overwhelmingly numerous details which research in this field daily brings to light, the resulting laws and general rules which first introduce order into the chaos of more or less misunderstood anatomical combinations.

First, having regard to our limited space, we will speak of the particular facts which belong to this part of the subject.

I have already more than once drawn attention to the radical change which the last few years has brought about in our conception of the structure of the central nervous system.

The idea, first formulated by *His* and *Forel*, that mere contiguity might be sufficient to connect the provinces of two separate nerve-cells, the ramifications of each fibre ending in free tips, won its way to general acceptance only when confirmed by facts revealed by the method of silver-impregnation and methylene-blue staining.

In the following observations we must take for our starting-point the nerve-unit, or neuron (see p. 127). We have seen that it consists of three principal parts (fig. 98, 1); first, the neurocyte or nerve-cell, I, with its dendrites (protoplasmic processes) and axis-cylinder process; secondly, the nerve-fibre, II, which arises from the cell through the axis-cylinder process,



and frequently gives off side-shoots (collaterals); and thirdly, the arborescent system or telodendrion, III, into which the fibre finally breaks up. The collaterals end in similar arborescent systems.

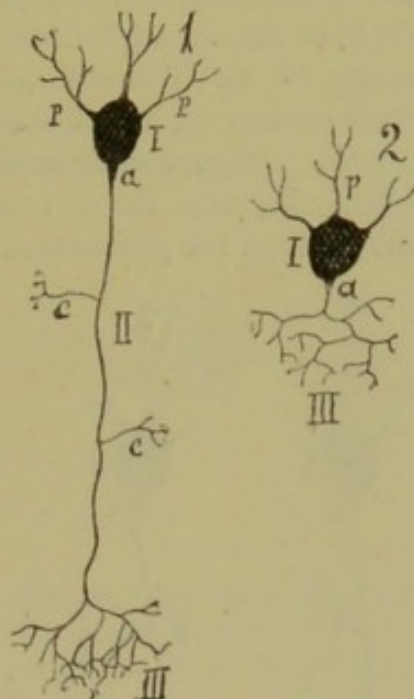


Fig. 98.—Diagrammatic representation of two neurons.—1. *I*, Nerve-cell; *p*, protoplasmic processes; *a*, axis-cylinder process, passing into the nerve-fibre, *II*, with its collaterals, *c*, and breaking up into the arborescent system, *III*. 2. Neuron of Golgi's second type, in which the axis-cylinder process, *a*, immediately breaks up into the arborescent system.

Deviations from the type are produced in various ways. As in fig. 98, 2, the length of the nerve-fibre may be reduced to a minimum, the axis-cylinder process breaking up into the arborescent system as soon as it leaves the cell. These are *Golgi's* cells, or the intercalated cells of *Monakow* (see p. 149). On the other hand, it sometimes happens that the nerve-cell is provided with two or more axis-cylinder processes (see fig. 57, p. 147), as is perhaps the case with the cells of the spinal ganglia.

We have next to investigate the manner in which the neurons enter into functional and anatomical relations with each other and with the organism as a whole. We will first consider the behaviour of the arborescent systems, since to them falls the office of establishing further relations between the neurons to which they belong.

(1.) The arborescent system may end freely at the periphery, perhaps in a muscle-fibre, *m*, (fig. 99, 1). As an example of this we may take a cell from the anterior horn of the spinal cord, with the motor nerve-fibre starting from it and ending in a peripheral muscle-fibre.

(2.) The arborescent process, III, of the first neuron may enter into relation with the nerve-cell, *I'*, of another (fig. 99, 2).

(3.) In addition to the relation exemplified in 2, the first neuron may be brought into connection with the cell, II, of a third by means of one of its collaterals (fig. 99, 3). Other collaterals or ramifications of the nerve-



fibre, II, may establish relations with yet other neurons. The type of behaviour represented in 2 and 3 is the commonest in the central nervous system.

(4.) Or the arborescent system, III, of the first neuron may enter into relation, not with the cell, I', of the second, but with the final ramifications of a protoplasmic process (fig. 99, 4). We have an example of this mode of connection in the bulbus olfactorius. I, would then stand for an olfactory cell, I', for a mitral cell of the bulbus, and we must suppose the interweaving of the arborescent system, III, with the end-ramifications of the protoplasmic process,  $p'$ , to take place in the glomerulus.

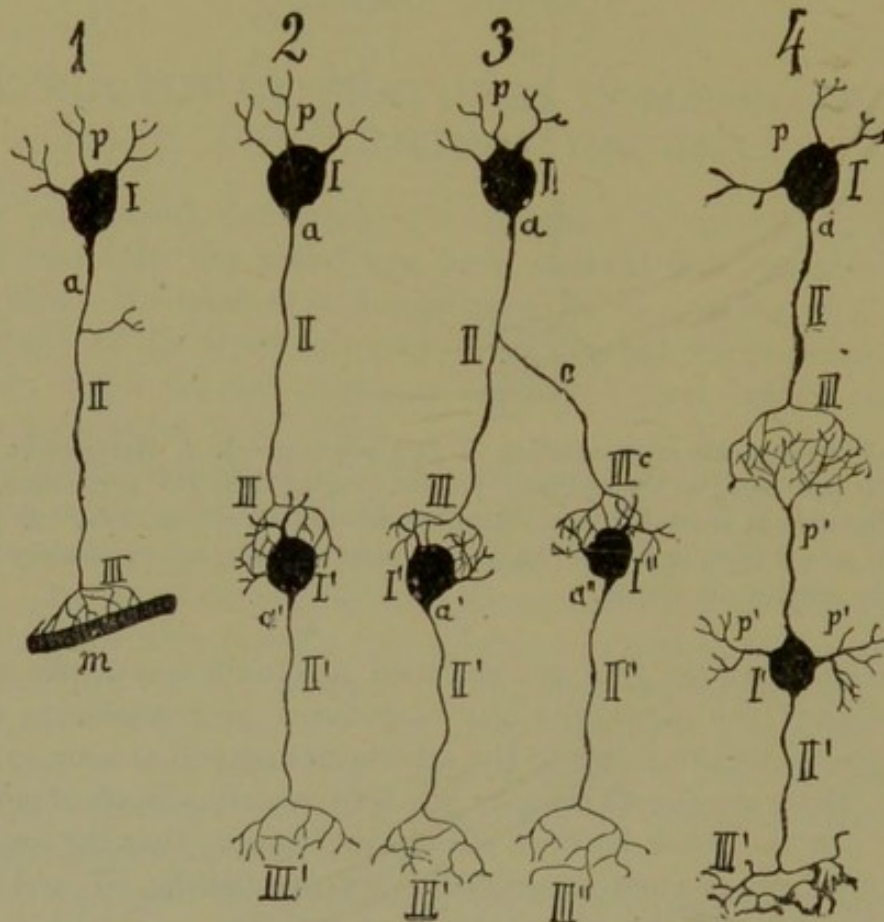


Fig. 99.—The various relations of neurons one to another.

(5.) Finally, it must not be forgotten that (in fig. 99, 4) the protoplasmic processes unconnected with the first neuron may have relations with other—third or fourth—neurons.

It has already been mentioned that, with few exceptions, the protoplasmic processes conduct in a cellipetal, the axis-cylinder process in a cellifugal direction. A very important exception to this rule is found in the peripheral process of the cells of the spinal ganglia, the peripheral sensory nerve-fibre. In many places, such as the mucous membrane of the olfactory organs, and the skin of animals low in the scale (worms), we find epithelial cells (sensory cells) in some respects homologous with the cells of the spinal ganglia. The peripheral process is reduced to a short stump, while the central process extends to the central organ. In other animals low in the scale the sensory cell sinks away from the epithelium, and its



peripheral process lengthens, until at last the bipolar cell with centripetal and centrifugal processes is produced which we meet with in the spinal ganglia of vertebrates, lying in the course of the sensory nerves.

This singular behaviour of the cells of the spinal ganglia has given rise to various attempts to fit them into the scheme of the other nerve-cells. It has been suggested, for instance, that the peripheral sensory nerve-fibre ought to be regarded as a dendritic process or a collateral, and the central root-fibre alone as an axis-cylinder process.

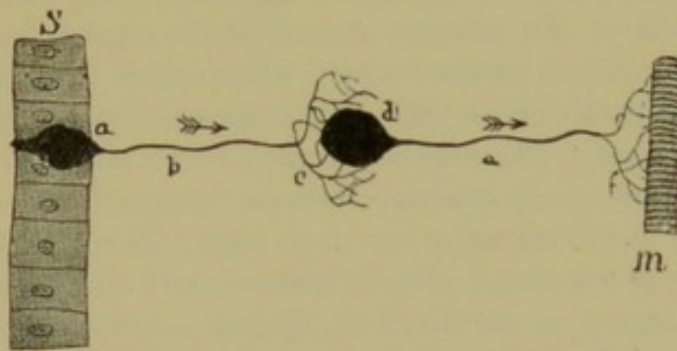


Fig. 100.—Scheme of the simplest form of nervous system.—*S*, Epithelium; *a*, sensory cell; *b*, centripetal sensory nerve; *c*, its arborescent system; *d*, cell of second neuron (motor nerve-cell); *e*, centrifugal motor nerve; *f*, its peripheral arborescent process in the muscle, *m*.

A diagram of the simplest nervous system may be constructed as follows (see fig. 100):—

In the peripheral epithelium of the body, *S*, lies the sensory cell, *a*, from which the sensory centripetal nerve, *b*, arises. Its arborescent process, *c*, lies close to the cell, *d*, of a second neuron. From the latter the centrifugal nerve, *e*, proceeds to the muscle-fibre, *m*, to which it affixes itself by its end-ramifications. Only two neurons are here represented, but each of them may stand for a group of neurons of equal value.

When we consider that the nervous apparatus is further complicated by the intercalation of other neurons, and by the manifold relations established by the dendrites on the one side and the collaterals on the other, we can well see that the multiplicity of nerve-connections almost defies imagination. It is even permissible to say that every part of the nervous system is in communication with every other part; the only differences among them being questions of intimacy of connection, without reference to topographical position. On the other hand, there are no isolated regions in the uninjured central nervous system—no islands which carry on their functions independently of the rest—although we are able to isolate certain regions with independent function by experimental methods, as, for instance, by transverse severance of the spinal cord, after which the caudal part may live and carry on its functions though completely separated from the rest of the central nervous system.

The nerve-cells are the real nerve-centres. To the fibres belongs only the task of conducting the stimuli transferred to them. Many other functions of the nervous system besides simple conduction belong to the



cells. The cells are the stations ; the fibres the railroads which connect the stations together.

The nerve-cells are not scattered about irregularly, nor do they occur singly in the nervous system ; but they cover, for the most part, extensive areas, in which they are collected in groups. In such places the character of the ground-tissue is also changed, the medullated nerves are mixed with many which are not medullated, the blood-vessels are very numerous and divide in a characteristic manner ; so that, even to the naked eye, such regions, rich in cells, present appearances by which they can be recognised. While those parts of the nervous system which consist almost entirely of medullated fibres exhibit an almost pure white colour (the white matter or medulla), the regions rich in cells are distinguished by different tints of red-grey or yellow-grey (the grey substance). The intensity of this colouring is not the same in all brains. Various circumstances combine to give the grey matter a darker or a less dark tint. The capillary net-work is closer in the grey substance than elsewhere, and hence the condition of the brain with regard to its blood-supply has a great influence upon its colour. Small, much-convoluted brains in which the pigmented elements are probably pressed closely together (as, for example, in cases of premature synostosis of the skull), contrast with the less fissured brains, showing often a strikingly strong colour in such parts of the grey matter as the cerebral cortex, nucleus caudatus, putamen, and cortex of the cerebellum. The brain of the negro is not darker than that of the white races. The brain is darkest in pathological conditions resulting from violent epileptic fits.

The tissues in those parts of the brain which are rich in nerve-cells but yet, owing to the preponderance of white fibres, do not exhibit the distinctive features of grey substance, is known as *substantia reticularis* (*formatio reticularis*).

All anatomico-physiological investigations must make the grey masses their starting points, and must next take up the question of the manner in which they are brought into connection with one another by the white tracts. This method of procedure cannot at all times be logically followed out, since there are many cases in which we have but a very superficial knowledge of the connections of the grey masses ; while, on the other hand, many groups of fibres cannot with certainty be traced to their destinations.

In comparing the grey masses of the central system with one another, the conclusion that they are not all of equal morphological value is forced upon us. We are not yet in a position to assign to each its place, but must be content with a classification which is in the main correct, and which we believe will never be altogether superseded, although as regards detail it may, by subsequent observations, be extended and completed.

The following kinds of grey substance must be distinguished :—

(1.) The cortex of the cerebrum which everywhere covers the surface of the secondary fore-brain.



(2.) The cortex of the cerebellum.

(3.) The region in which the peripheral nerves originate, or end, namely, the grey masses in the spinal cord, and the corresponding portions of the brain from which the cranial nerves take origin. With these grey masses may be included the inner lining of the third ventricle which is their direct continuation, although it does not give origin to any peripheral nerves. These grey structures are summarised by *Meynert* in the expression 'central cavity-grey' (centrales Höhlengrau). They are the proper primary central grey masses of the nervous system to which the other organs arranged in the classes 1, 2, and 4 are but adjuncts.

It must always be borne in mind that there is an essential difference between the motor and sensory nuclei. While the nerve-cells of the motor nuclei (nuclei of origin) do as a matter of fact give rise to the motor nerve-fibre by means of the axis-cylinder process, the sensory nerve-fibres originate in cells which lie outside the central nervous system. The sensory root-fibres end in the cells of the nuclei in question (end-nuclei), which occupy the position of termini to them.

(4.) The central ganglia. Theoretically this group is well defined, since it includes all structures which do not find a place in classes 1 to 3; so heterogeneous a group does it make, however, that it is best to regard it as a temporary association of elements which cannot be otherwise classified.

Just as in the grey masses so also in the white we can recognise distinctions, but these after all depend upon the arrangement of the grey masses. Every fibre may be regarded as a conducting path either connecting two nerve-cells or a nerve-cell and a peripheral end-organ, be it motor or sensory. As each terminal apparatus is independent and endowed with a well-defined function we may regard it as of equal value, physiologically, with a nerve-cell. Indeed an end-organ may be looked upon as the terminal station of the road which extends outwards from the nerve-network.

Topographically nerve-fibres may be separated into two large groups—

(1.) *Fibræ homodesmoticae*; or fibres uniting together two homologous points of similar grey masses, as, for example, the two anterior cornua of the spinal cord or two spots in the cortex of the cerebrum.

(2.) *Fibræ heterodesmoticae*; which bring into connection two grey masses of unequal value, or else unite a central region with an end-organ. It is possible further to subdivide this group, as, for example, into fibres connecting the cerebral cortex with the central ganglia, fibres connecting the periphery with the nuclei of origin, etc.

The physiological importance of these distinctions needs no explanation.

The term **tract** is used to signify the connecting road between two central grey masses, or between a grey mass and an end-organ. We have almost always, however, to do with a more or less complicated combination of roads, bringing stations of several different distances apart into functional relation with one another. Hence, for example, we may speak of a cortico-muscular tract, meaning thereby the whole group of nerve-fibres (perhaps interrupted at more than one point by the intercalation of grey



masses), along which an impulse starting in the cortex must travel, if it is to induce a movement in a certain muscle. In the same way we speak in common life of the Berlin and Vienna Railway, although we know quite well that Dresden and Prague lie between the two termini.

Following this comparison a little longer. The route just mentioned is by no means the only connection between Berlin and Vienna; not only can we take the line through Breslau and Oderberg, avoiding Dresden and Prague, but various alternative routes from Berlin to Dresden, or from Prague to Vienna, are offered to us; further, we are in a position to go direct from Dresden to Vienna without touching at Prague, and so forth. When, for example, it happens that owing to a landslip the line between Dresden and Prague is impassable, the connection between Berlin and Vienna is not thereby interrupted. The richer the network of rails the more numerous are the connections, the 'tracts' between the two chief termini.

Now let us transfer these observations to nerve-tracts. The most highly specialised nervous system, capable of performing the greatest variety of functions, is the one in which the paths connecting its grey masses are most numerous. The corpus callosum is a striking example of this law. In birds it is almost wanting, in animals lower than birds it is very small; it only attains to its highest development in Man [*cf.* p. 86].

From this follows a result not difficult to prove by gross anatomy. The higher the animal the greater is the quantity of white substance, relatively to the grey, found in its central nervous system.

Since the cells of the grey substance are the true apparatus of the higher cerebral functions, it might be inferred, *a priori*, that the higher the intellectual development of the animal the greater would be the relative amount of grey substance; the perfect action of the brain depends, however, upon the most intimate association possible of all its centres with one another.

*Danilewsky* has shown this changing relation of the white substance to the grey by a chemical method.

Another lesson may be learnt from the railroad illustration. Supposing the line between Dresden and Prague is interrupted, I can still, if I choose, adopt a method, somewhat slower, perhaps, of travelling from the one place to the other, at all events until the new line is in working order. So, too, in the central nervous system, when one track is interrupted other collateral routes are still at our command. It would be quite wrong to conclude that, because a function is still performed after certain fibres are destroyed, those fibres have nothing to do normally with the conduction of the said impulses.

It follows that one must be very careful in assigning an object to nerve-routes, especially when they exceed an internode (the distance between two nerve stations) in length.

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It has already been mentioned that we have to distinguish two kinds of nerve-fibres from one another—the homodesmotic and the heterodesmotic fibres uniting co-ordinate and subordinate grey masses respectively. A further distinction between the fibres depends upon whether they unite together centres lying on the same side only, or, by crossing over in the middle line, bring into connection stations which lie in opposite halves of the body. Either class of fibres may cross in the middle line—homodesmotic fibres when crossed constituting a **commissure** (fig. 101,  $c c'$ ), heterodesmotic fibres a **decussation** ( $c g'$  and  $c' g$ ).

Here we may remark that the central nervous system appears to be symmetrical in structure as far as the main lines on which it is laid down are concerned. Excluding purely teratological or pathological differences between the two sides, however, certain striking, although inconstant, deviations from symmetry are exhibited, especially between the two sides of the great brain. Deviations from symmetry are commoner, and more conspicuous in highly developed brains than in those lower in the scale.

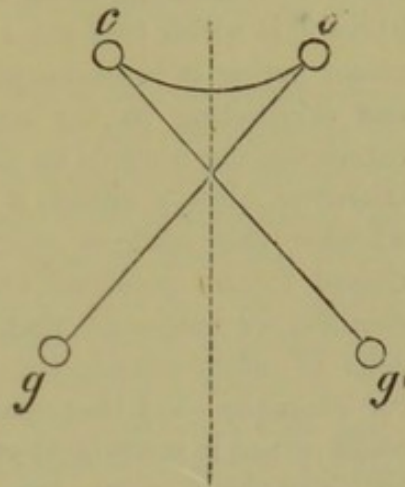


Fig. 101.— $c$  and  $c'$ , Cells of the cortex;  $g$  and  $g'$ , nerve-cells of a different category;  $c c'$ , commissural fibres;  $c g'$  and  $c' g$ , decussating fibres.

By **nucleus** is meant, in a general sense, a group of nerve-cells within the central system. In a particular sense the word is used to indicate the nucleus of a nerve; since in such cell-groups peripheral motor nerves commence and sensory nerves end.

One or more nuclei (which form part of the grey masses classed on p. 197 as group 3) belong to each peripheral nerve. It has never been proved in a single case that a nerve-fibre runs directly from the periphery to the cortex cerebri; the same assertion may be made with the highest degree of probability in the case of the cerebellar cortex.

The expression **nerve-root** is used in two quite different senses, likely to give rise to misapprehension; each use of the term is, however, so thoroughly naturalised that it would be very difficult to displace it.

By 'nerve-root' is meant in gross anatomy the bundles of fibres by

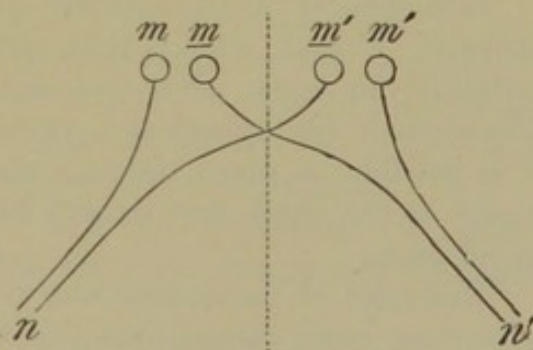


Fig. 102.— $n$  and  $n'$ , Motor nerve-roots;  $m$   $\underline{m}$ ,  $\underline{m'}$  and  $m'$ , cells of the nuclei of origin of the two sides;  $m$  and  $m'$  for the uncrossed,  $\underline{m}$  and  $\underline{m'}$  for the crossed fibres.



which the nerve appears to come out from the brain or cord, which bundles seem, therefore, to be the commencement of the nerve, the *peripheral root*. On the other hand, the fibres by which, within the central system, the nerve is continued to its nucleus are known as the *central root*. These fibres it is which lead the nerve back to its real origin or end. For many motor nerves it has been ascertained that they have two sets of root-fibres, one originating in the nucleus on the same side and the other in the corresponding nucleus on the other side of the body. A part of the nerve; therefore, always enters a decussation. It has not yet been determined whether this mode of origin is common to all motor nerve-roots. With regard to the posterior nerve-roots, which are almost without exception sensory, we may note that certainly the greater part of them have their cells of origin outside the central nervous system—in the spinal ganglia, for example—but that a small proportion of fibres (whether in all sensory roots or not is uncertain) originate within it. The trigeminus arises from two peripheral roots, but has at least six roots which run within the cerebro-spinal axis.

Every nucleus of a peripheral nerve is connected with other parts of the central nervous system. The paths by which these various connections are maintained may be classified as follows:—

1. Connections with the corresponding nucleus of the opposite side ;
2.     ,,         with other nerve nuclei ;
3.     ,,         with various secondary ganglionic centres ;
4.     ,,         with the cortex cerebelli ;
5.     ,,         with the cortex cerebri, directly or indirectly (as in fig. 99, 2).

Commissural fibres between corresponding nuclei of the two sides probably always exist; they are only demonstrated with absolute certainty for some nerve-centres; for example, the oculomotor nuclei (*Nussbaum*), the hypoglossal nuclei (*Koch*), etc. *Flehsig* believes that it is possible to prove the existence of commissural fibres between the nuclei of the three first sensory nerves, and infers that such fibres exist in all cases.

Examples of the connections with dissimilar nuclei (class 2) are very numerous, some crossed, but the majority not crossed. The 'posterior longitudinal bundle' was formerly supposed to consist of fibres connecting together nuclei, which lie one behind another.

Connections with secondary ganglia (3), as the thalamus, corpora quadrigemina, corpora geniculata, olive, and so forth, are proved in many cases, and may well obtain in all without exception.

How the cortex cerebelli (4) is connected with the nuclei of origin of sensory nerves is by no means always clear; *Marchi* is of opinion that it is by the posterior longitudinal bundle. But in the case of the spinal nerves and a part of the auditory nerve, we think we know the route by which a



connection is established. *Edinger* designates the fibres which pass to the cerebellum from a number of sensory nerves collectively the 'direct sensory tract' of the cerebellum.

An undeniable direct connection between the cortex cerebelli and a motor nerve-nucleus has yet to be found.

Especially interesting, both from an anatomical and a physiological point of view, are the so-called central connections of the nerve-nuclei (5), the tracts, that is to say, by which they are connected with the cortex cerebri. In all cases the connection is supposed to be a partly crossed one, but it is extremely difficult to ascertain the relative numbers of the crossed and uncrossed fibres. Probably the proportion is not the same in any two nerves. For many of the nerves belonging to the hind-brain we have to seek these crossing fibres in the *fibræ arcuatæ* (including the *striæ acusticæ*); the fibres cross one another in the raphe at a very acute angle. From the cells of the sensory end-nuclei fibres arise which conduct directly or indirectly to the cortex of the cerebrum; sensory tracts of the second class. Many of these fibres seem to give off collaterals which spread out to other, motor, and perhaps sensory nerve-nuclei, and thus establish an internuclear connection.

We may hope to come to a better anatomical and physiological understanding of the central nervous system when we have learned to classify the, at present, almost incomprehensible mass of details, with such order and method as will doubtless be made possible by further observations.

When we are able to speak of structures in groups which now seem to exact individual treatment, a clearer general view of the system will be obtained. The optic tract, for example, is, in a certain sense at least, homologous with the fillet tract. When this homology is further traced we shall come to a clearer understanding of the meaning of many structures which are in connection with the optic tract.

It is undesirable to press homologies too far, although a scheme embodying the main features of the central conducting paths is of inestimable value. We recognise at once departures from what we consider the normal arrangement, and seeking to account for these deviations, we discover the faults in our scheme and the real explanation of these differences.

The relations exhibited in a simple form by the spinal cord yield information which we may use in studying the more complicated medulla oblongata and brain.

Motor-spinal and motor-cranial nerves may be supposed to present similar central connections; a parallelism may likewise be traced in the case of the sensory nerves in the two regions respectively. This consideration makes it possible for us to throw light into many dark places. It affords us many hints as to the objects we should have in view in anatomical investigations, and as to the connections of fibres which seem to be physiologically necessary, or which we should expect from analogy to be present.

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The great variety manifested in the course of the several central nerve-bundles, and the consequent difficulty of gaining a clear conception of their arrangement, have long since led observers to attempt a generalisation or schematisation of the apparent chaos. In the foregoing pages I myself have often been obliged to have recourse to some such simplified representation, as for instance in the diagram of the simplest form of nervous system.

For a right understanding of the nerve-roots *Sir Charles Bell's* distinction between sensory and motor roots is of the highest importance, but it is neither sufficient nor can it be pressed too far. *Bell's* original division into two classes has therefore been greatly modified and supplemented. *A. Hill* has propounded a four-root theory. According to this, the anterior roots of the spinal cord contain fibres of three kinds, proceeding from the cells of the anterior horn, the lateral horn, and Clarke's columns respectively. To each kind different functions are allotted, all in the motor region. The posterior spinal roots contain sensory fibres. The same scheme applies to the cerebral nerve-roots, though their various fibres are naturally subject to many displacements. Thus, the root-fibres which correspond to the actual nerves of the anterior horn come out in the N. hypoglossus and the nerves of the eye-muscles; while the fibres which originate in the lateral horn are represented by the N. accessorius, the motor part of the N. vagus and glossopharyngeus, the N. facialis and the motor root of the trigeminus.

The difficulty in elaborating a simple and comprehensive scheme of the construction of the nervous system depends upon the great variety of elements which must be ranged in their places; if all varieties are allowed for, a perplexing and highly complicated scheme is the result.

Many difficulties have to be overcome before a scheme satisfying all our requirements will be produced. This is, however, the place to sketch in outline some of the generalisations on this subject.

*Lays* takes his starting point, erroneously, from the central ganglia of the great brain (nucleus caudatus, nucleus lenticularis, and optic thalamus); they form the proper central point, towards which all nerves converge from the two sides. There are two principal systems of converging fibres—(1) 'fibres convergentes inférieures,' including all the fibres which travel from the periphery to the central ganglia, without regard to the direction in which they conduct; and (2) 'fibres convergentes supérieures,' including all the cortical fibres, for these in a similar way seek the central ganglia. All fibre-roads of the first category are broken on their way to the ganglia by still other grey masses. All cross the middle line, although the fibre-systems of the two sides of the body remain distinct from one another. The other kind of fibres, 'fibres convergentes supérieures,' pass without crossing and without interruption from the cortex to the ganglia. They are united, however, with those of the opposite side by a special commissural system.

*Meynert*, in formulating his scheme, commences with the cortex of the great brain, as being the organ devoted to conscious processes. All routes



which serve as media of communication between the cortex of the cerebrum and the outer world are grouped together in a chief system. Through the fibres of this system sense-pictures are projected on the perceptive cortex; and, further, not only are movements of one's own body the source of sensations of movement which are represented in the brain in the same way as phenomena of the outer world, but the cortex also, by means of the motor-tracts, reflects outwards again the states of stimulation, information with regard to which is transferred to it by means of sensory nerves. These conducting paths Meynert, therefore, terms collectively a 'projection system.'

The cells of the cortex are connected with the corresponding cells of the opposite side by 'commissural-systems' and with cells of distant parts of the same hemisphere by 'association-systems.' The medullated fibres which connect the lobes of the great brain with the cortex of the cerebellum fall into a special class.

The 'projection system' is divided into segments by the intercalation of two kinds of grey matter. The first segment consists, for the most part, of fibres radiating from the central ganglia to the cortex—the corona radiata. The second segment extends from the basal ganglia to the grey matter surrounding the central cavities in the peduncular system. The third segment of the projection system is made up of the peripheral nerves which have their origin in the grey matter bordering the cavities from the aqueduct of Sylvius down to the end of the spinal cord.

A. Hill's scheme is simple. He argues that the central nervous system consists fundamentally of but two parts, or tissues, the older plexus of grey matter accumulated in the vicinity of the central canal (the 'central grey tube') and the more recent and more plastic mantle of grey matter which covers the surface of the cephalic vesicles (the 'peripheral grey tube'). These two tubes are connected by cell-processes, which, protected by medullary sheaths, make up the mass of white matter which intervenes between the central and peripheral tubes. The central grey tube is in direct relation with both anterior and posterior peripheral roots. Its plexus is divided metamerically into 'centres' for nerves. It includes the optic thalami. The peripheral grey tube comprises two chief fields of cortex, the cerebellar and cerebral mantles, connected by afferent and efferent fibres with the several metameric clumps of the lower or central grey tube. It is, therefore, itself divided into areas connected *indirectly* only with the several peripheral nerves.

The above is a superficial survey of the schemata of Meynert, Luys, and Hill; it is hardly possible to give an account of other views as to the plan of the nervous system. Aebly takes his stand upon the segmental constitution of the spinal cord, each metamer of which belongs to an anterior and posterior root. In the brain a similar segmentation may be traced, but it affects the stem region only, not the cortex. Aebly analyses the relations of the grey masses and the tracts of fibres on this basis.

Flehsig has designed a 'plan of the human brain,' but it is impossible to reduce his views to an abstract; it may just be mentioned in this place



that he summarises the conducting paths in the four following chief systems:—(1) the (relatively) direct connection of the cortex with motor and sensory nerves; (2) system of the optic thalamus; (3) system of the pons; (4) system of the tegment, to which belong the fibres of the corpora restiformia, as well as certain columns of the spinal cord.

## I. TOPOGRAPHY OF THE SPINAL CORD.

The internal structure of the spinal cord is best studied by means of sections of the hardened organ cut transversely. The comprehension of the anatomical relations of its several parts is, however, aided by studying sections cut in other planes. For example, pieces of the spinal cord from the cervical or lumbar enlargement, of from 1 to 1.5 cm. long, are cut into sagittal sections (antero-posterior sections parallel to its long axis). Frontal sections (from side to side, but parallel to the long axis) are also prepared. Oblique sections may be useful under certain conditions; such can be cut in the plane of entry of the posterior roots for example. A series of these longitudinal sections should be made, not necessarily unbroken, but containing at least fifteen or twenty specimens from the half of a single cord. They are best mounted on collodion plates (see p. 12). Where the preparations are not required to be histologically faultless it is advisable to let the cord lie for from three to six weeks in chromate of potassium and subsequently in alcohol, and to embed in celloidin. Freshly-prepared chromic cords of animals (horse, ox, etc.) give beautiful preparations, even without hardening in alcohol and embedding in celloidin. They furnish the best material for fine carmine preparations, and for the study of many minute questions of structure.

The structure of the cord changes from region to region; therefore it is desirable to study a large number of sections taken at intervals from the whole length of the cord, in order that one may be enabled to recognise approximately the level from which a given section was taken. The lowest magnification suffices to arrange these sections in their order. We shall, therefore, first describe the appearances of sections as seen under a weak objective.

It is best to make two parallel series of sections in this, as in many other investigations, treating each series *secundum artem* with a special method of staining. The one series is coloured with alum-hæmatoxylin and then with carmine, or with carmine or nigrosin alone;—in all cases except such as involve pathological changes it is sufficient to stain the nuclei of a section here and there with alum-hæmatoxylin. In view of the uncertainty of carmine staining it is well worth while to try *v. Gieson's* method, which generally proves an excellent substitute. The other series is coloured by one of the methods of medullary-sheath staining described on pp. 19 *et seq.*; and in some cases further treated with other staining-agents. Of course this does not exclude the occasional employment of



other approved staining-methods. Thus, the number and position of the nerve-cells can be most plainly seen by hardening in alcohol and staining with methylene-blue by Nissl's method (p. 16). It is not necessary to adhere strictly to all the cautions he gives, the less so as the object in view is not an examination of the minutest details of structure.

Many important details of the internal structure of the spinal cord can only be observed by the application of the silver method of impregnation to embryonic tissue. Unfortunately, the materials for such investigation are not always to hand, and in many cases the personal observation of the student must necessarily be confined to such facts as can be gathered from other methods of preparation.

In the ordinary method of taking the brain out of the skull-case, the spinal cord is usually cut across at the level of the second or third cervical nerve.

We will commence our description with a section through this region (fig. 103, half of the cord only represented). Transverse sections of the cord should always be drawn with the ventral half downwards, if for no other reason yet because it is necessary to observe this arrangement at the transition to the medulla oblongata and at higher levels. In the first place we notice that a complete section is divided into two almost symmetrical halves. On the ventral side the fissura longitudinalis ventralis, *Fsla*, sinks into the substance of the cord. After reaching in depth about a third of the antero-posterior diameter, it splits into two short lateral divisions. From the sulcus longitudinalis dorsalis, *Fslp*, a gleia-septum (septum medianum dorsale, *Smd*) dips inwards about half as far again as the ventral fissure, which it almost meets. Only a narrow bridge of nerve-substance which unites the two halves of the grey matter together, the commissura medullæ spinalis, *Com*, intervenes between the two fissures.

The commissure falls into two well-marked divisions, the anterior or white commissure on the ventral side, the grey commissure on the dorsal. The latter is again divided into the commissura grisea anterior and the commissura grisea posterior by the central canal with its envelope of substantia gelatinosa centralis, which lies in the middle of it.

The white investing sheath and the central grey substance are clearly differentiated in the spinal cord.

The grey matter on either side of the section we are now considering appears as an elongated area with its long axis placed almost sagittally; in the dorsal half it bends a little sideways. The grey masses of the two hemispheres, taken together, make an **H**, the cross bar of which is formed by the grey commissure. The larger part of the grey matter lies on the ventral side of the cord, and is known as the anterior horn, *Cra* (cornu anterius), the more slender portion is directed backwards as the posterior horn, *Crp* (cornu posterius).

Considered in their continuity the anterior and posterior horns, extending as they do as veritable columns throughout the whole length of the spinal cord, may well be termed, as is often done, the anterior and posterior columns.



The short lateral bulging of the grey matter opposite the commissure is pointed out as the lateral horn, *Til* (middle horn, tractus intermedio-lateralis). The re-entrant angle between the posterior and lateral horns is filled in with trabeculae of grey substance, between which room is left for the passage of columns of fibres; the network of grey strands constitutes the processus reticularis, *Pr* (by many persons, *Goll* for instance, termed the lateral horn).

The anterior horn is round, while the posterior horn is fusiform in shape. The much drawn-out point of the spindle (apex cornu posterioris, *Ap*) looks as if it were continued to the sulcus lateralis dorsalis. The posterior horn never actually reaches the surface of the cord; at every level we find an intervening tract of white matter, called by *Lissauer* the marginal zone, by *Waldeyer* the medullary bridge. It is connected with the rest of the grey matter by the basis cornu posterioris; dorsal to the base, it is constricted into a neck [cervix cornu posterioris], while the real body of the spindle is known as the head [caput cornu posterioris].

Two kinds of grey matter are usually distinguishable from one another under low magnification, when the preparation is stained with carmine—substantia spongiosa and substantia gelatinosa.

In preparations made by Weigert's method or Pal's the substantia spongiosa stands out in pale-grey from the blackened medulla, the substantia gelatinosa remains almost uncoloured. Carmine and nigrosin give the substantia gelatinosa the darker colour.

The latter is limited to two regions—(1) immediately around the central canal (substantia gelatinosa centralis); (2) in a part of the posterior horn where it forms the cap on the top of the caput cornu posterioris (substantia gelatinosa Rolandi, *Sg*). Dorsally it extends into the apex, while it is concave ventrally. The spongy substance is far more considerable in amount.

The anterior roots, *Ra*, are seen springing from the anterior horn; they take their exit in several (3–8) thin bundles of medullated nerves which traverse the white substance in a horizontal plane while distinctly curving outwards in their course. Even with the least magnification it is possible to see in the anterior horn the large nerve-cells which give origin to the fibres of the anterior roots. These do not fall into sharply-defined groups. Conspicuous on the mesial margin of the anterior horn is sometimes a peculiar group of longish cells, the commissure group of *Lenhossék*. A group of smaller cells, more closely pressed together, is seen in the lateral horn. Large cells are scattered in the processus reticularis. *Waldeyer* gives the name of 'middle cells' to a group at the base of the posterior horn. It can be seen most clearly in the cervical medulla, on the ventral side of the respiratory bundle (to which I shall presently refer), but may be followed downwards as far as the lumbar region. Single cells, generally of inconsiderable size, are found in various parts of the grey substance. From the region of the processus reticularis in some sections at this level (although not in the particular one which is now being described) distinct bundles of nerves are seen coursing towards the periphery in arches



directed dorso-laterally. These are the root-fibres of the nervus accessorius Willisii.

The dorsal or posterior nerve-roots, *Rp*, are seen entering the posterior horn at the sulcus lateralis dorsalis, *Sld*. Part of their fibres can be followed to the mesial side of the posterior horn, another part streams directly into the substantia gelatinosa Rolandi. The fibres of the first group describe, in their course through the posterior column, more or less open arches, and seem to sink into the grey substance of the posterior horn, in which they can be followed ventrally for a considerable distance.

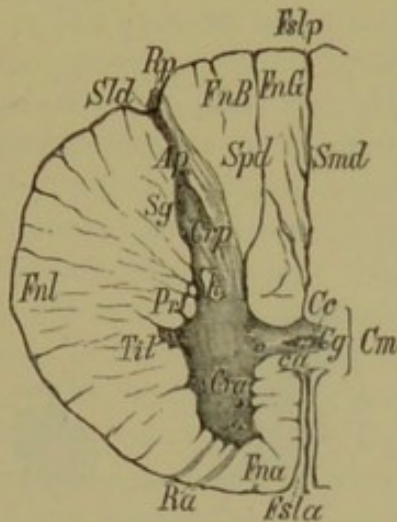


Fig. 103.

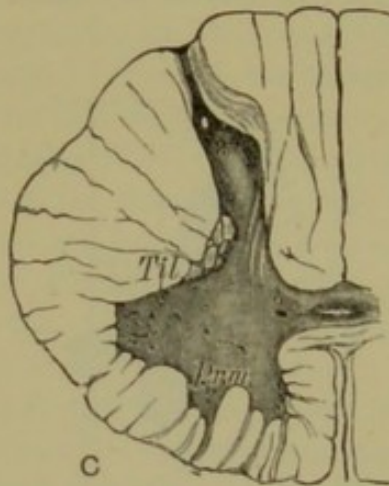


Fig. 104.

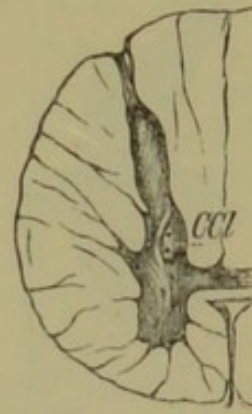


Fig. 105.

Figs. 103-109.—Transverse sections through the human spinal cord. Carmine staining. Magn. 5.

Fig. 103.—Section at the level of the third cervical nerves.—*Fsla*, Fissura longitudinalis anterior; *Fslp*, fissura longitudinalis posterior; *Fna*, anterior column; *Fnl*, lateral column; *Fnb*, Burdach's column; *Fng*, Goll's column; *Smd*, septum medianum dorsale; *Spd*, septum paramedianum dorsale; *Sld*, sulcus lateralis dorsalis; *Rp*, radix posterior; *Ra*, radix anterior; *Cra*, anterior horn; *Crp*, posterior horn; *Trl*, tractus intermedio-lateralis; *Pr*, processus reticularis; *Sg*, substantia gelatinosa Rolandi; *Ap*, apex; *k*, respiratory bundle of Krause; *Cm*, commissura medullae spinalis; *Cg*, commissura grisea; *ca*, commissura alba; *Cc*, central canal.

Fig. 104.—Transverse section at the level of the sixth cervical nerves.—*Prm*, Processus cervicalis medius cornu anterioris; *Til*, lateral horn.

Fig. 105.—Transverse section at the level of the third dorsal nerves.—*Ccl*, Clarke's vesicular column.

The white substance of the cord is usually divided into several columns.

(1.) The posterior column (dorsal column, *Kölliker*), which extends on either side of the septum medianum dorsale as far as the posterior horn. A constant septum of gleia (septum paramedianum dorsale, *Spd*) starts at the surface and passes inwards with an inclination towards the median septum, and often gives off a branch directed outwards towards the posterior horn. It splits the posterior column into two well-defined subdivisions, of which the mesial or smaller is termed Goll's column or the funiculus gracilis, *Fng*, the larger one is Burdach's column or funiculus cuneatus, *Fnb* (ground bundle of the posterior horn).

(2.) The lateral column, *Fnl*, usually considered as extending from the



outer margin of the posterior horn to the most laterally situate bundle of the anterior root.

(3.) The anterior column, *Fna*, surrounding the ventral and mesial surfaces of the anterior horn.

It has been recognised for a long time that the division between the anterior and lateral columns is an artificial one, and hence they are often united under the name of antero-lateral column (ventral column, *Kölliker*).

In addition to the three white columns already mentioned, the white commissure, *ca* (commissura alba), still remains to be described. It lies on the ventral side of the grey commissure, and forms a narrow bridge across from one of the anterior columns to the other.

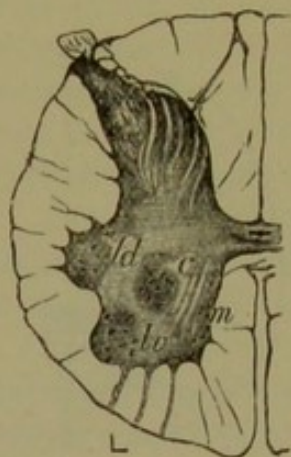


Fig. 106.



Fig. 107.



Fig. 108.



Fig. 109.

Fig. 106.—Transverse section at the level of the twelfth dorsal nerves.—*m*, Medial; *lv*, latero-ventral; *ld*, latero-dorsal; *c*, central groups of cells of anterior horn.

Fig. 107.—Transverse section at the level of the fifth lumbar nerves.—*CCI*, Clarke's column.

Fig. 108.—Transverse section at the level of the third sacral nerves.—*m*, Medial; *ld*, latero-dorsal group.

Fig. 109.—Transverse section through the inferior part of the conus medullaris at origin of nervus coccygeus.

Lastly, a small, but often very conspicuous, bundle of nerve-fibres is cut transversely in this section (the respiratory bundle of *Krause*, *k*), which lies in the basis cornu posterioris on the mesial side of the processus reticularis. It is not always easy to distinguish from other nerve bundles in that region.

If we now muster our sections in order from the third cervical to the end of the spinal cord we meet with changing conditions, subject, however, to not inconsiderable individual variations.

At the fourth cervical the picture presented by a section is almost the same as at the third, save that, on close inspection, a commencing enlargement of the anterior horn is perceived. At the fifth cervical the enlargement becomes more pronounced. The total cross-section of the cord is by this time obviously increased, especially in its transverse diameter. It has assumed an elliptical form, the amount of eccentricity of the ellipse being very variable. Root-bundles of the accessorius are no longer distinguishable.



The cervical enlargement reaches its maximum at the level of the sixth cervical nerve (fig. 104). Here the anterior and lateral horns are fused together into a considerable mass, forming in cross-section an equilateral triangle. A little grey protuberance (processus cervicalis medius cornu anterioris, *Prm*) projects from the middle of the ventral side of the anterior horn, giving it a triangular shape. A group of large nerve-cells is seen in each corner of the triangle. Although the anterior and lateral horns are fused together it is usually possible to recognise, near the dorsal border (formerly the lateral border) of the anterior horn, the closely aggregated cells of the former lateral horn, *Til*.

The posterior horn has also increased in size, but not so obviously as the anterior, without, however, losing its elongated form. Still it must be pointed out that the increase in size of the posterior horn is almost restricted to its mesial side, so that now the apex rises with a step from the posterior column, a peculiarity which (despite many changes in form) it retains throughout the rest of the spinal cord. The lateral inclination of the posterior horn now becomes less marked, its long axis lies more parallel to the dorso-ventral diameter of the medulla. The processus reticularis loses in development, and so, too, does the so-called respiratory bundle.

The cervical enlargement is still at a maximum at the level of the seventh cervical nerve, beyond the eighth it gradually decreases. The processus cervicalis medius (which is sometimes lacking even in the region of the seventh) sinks away and the ventral side of the anterior horn is bounded instead by a slightly concave line.

At the level of the first dorsal nerve the lateral horn grows rapidly smaller, at the same time retiring mesially until, between the seventh and eighth it projects like a beak from the lateral border of the grey matter (fig. 105). The characteristic group of cells which constitute the lateral horn is extended towards the posterior horn. Thus it comes about that the total cross-section of the grey matter again assumes the form of the letter **H** which we remarked in the upper cervical region; the two sections are, however, easily distinguishable, for the one from the dorsal region has the characteristic features which we have just remarked—its grey matter is narrower and more slender, the respiratory bundle is absent, the processus reticularis poorly developed, the posterior horn, directed a little outwards, rises by a step on its mesial side. At the same time the main body of it retreats noticeably from the periphery, with which it is connected by a narrow streak. At the level of the seventh or eighth cervical a group of cells, not found at higher levels, makes its appearance in the basis cornu posterioris, near its mesial border, *COL*. The fibres of the posterior roots arch around this column. In it are contained at first only scattered cells of large size. It has been named Clarke's column (columna vesicularis, dorsal nucleus of *Stilling*). Only in the dorsal region do the cells of this column constitute a well-defined group which causes a mesial bulging of the posterior horn. In many preparations of the upper dorsal cord these cells are altogether absent. In many spinal cords, on the other hand, we meet with single cells, running far up into the cervical medulla,



in a position corresponding to that occupied by Clarke's columns in the dorsal region. *Waldeyer* calls these 'Stilling's cells.'

Except for the slow increase in size in Clarke's column from above downwards, it is impossible to distinguish the several sections of the dorsal cord from one another. Clarke's column is best developed at the eleventh or twelfth dorsal, and at this level the total amount of grey substance begins again to increase; this is the commencement of the lumbar swelling (fig. 106). Here the posterior horn again inclines outwards, recalling the disposition in the cervical cord; the great size of Clarke's column, however, and the relatively broader mass of grey substance, allow of no mistake.

In the region of the cord, from which the lumbar nerves come off, the cross-section of the grey matter increases both in the anterior and the posterior horns. Nevertheless, the total size of the cord in the lumbar region can never equal that of the cervical enlargement, for the constantly diminishing amount of white matter observed in descending the cord tells in the total cross-section. The difference in relative amount of grey and white substance is obvious (fig. 107). The section is nearly cylindrical in this region.

In comparison with its shape in the cervical region the anterior horn is noticeably more rounded. So, too, is the posterior horn, the main mass of which, owing to the shortening and thickening of the apex, approaches nearer to the dorsal surface. At the fourth, and still more at the fifth, lumbar nerve where the grey matter is most abundant the lateral horn again acquires a certain amount of independence after having been involved in the upper lumbar region in the rounded enlargement of the anterior horn. Here, too, the large nerve-cells are more distinctly collected in groups than anywhere else. Their arrangement, however, is not quite constant, and hence they have been variously described. Between the second and third lumbar nerves Clarke's column again disappears almost completely, though in exceptional cases it is represented lower down by isolated cells. In the anterior horn the cells are arranged as follows:—

1. A rather small mesial group (the commissural group, *m*), not very well defined, to which the whole of the mesial border of the anterior horn belongs. It consists almost entirely of fusiform cells arranged with their axes in a sagittal direction.

2. A latero-ventral group (*Lv*).

3. A latero-dorsal group (*Ld*).

4. A middle-group (*c*) almost in the centre of the anterior horn.

The general appearance of the cross-section is somewhat changed, owing to the anterior longitudinal fissure cutting more deeply into the substance of the cord, whereby the anterior commissure is carried almost to the middle of its sagittal axis. The septum paramedianum is often wanting below the lower dorsal nerves.

From the point of exit of the lowest fibres of the anterior root of the fifth lumbar nerve in the conus medullaris, the spinal cord rapidly diminishes in size until it terminates in the filum terminale. The white sheath diminishes much more quickly than the central grey masses, which



rapidly obtain the preponderance. In most cords we notice that the mesial part of the posterior column is separated from the dorsal by a septum, and is either simply depressed on the dorsal periphery, as in fig. 108, or, more commonly, forms a rounded projection at the bottom of a groove. This formation is not analogous to Goll's column in the upper portion of the cord, but is a fibre-tract of distinct character, the fasciculus dorso-medialis sacralis.

The form of the grey horns is not much altered, but they become plumper; the posterior horn especially appears more uniformly rounded. The grey commissure becomes broader and approaches nearer to the posterior surface, at the level of the lowest sacral nerves, where the cord scarcely attains 4 mm. in diameter; but little room is left for the posterior columns.

Of the several groups of nerve-cells described above, only the latero-dorsal group, *Ld*, and the mesial group, *m*, remain by the time the third sacral nerve is reached (fig. 108). At the level of the fourth sacral nerve no distinct groups, but merely large scattered cells, are seen. In many cords a group of cells representing Clarke's columns (Stilling's sacral nucleus) reappears at the base of the posterior horn.

Even at the end of the conus medullaris (fig. 109), the region from which the nervus coccygeus springs, the typical formation of the spinal cord is evident. The filum terminale is nothing but a tube of epithelium with a thin covering of grey substance, the last remnants of the central grey matter of the cord. The lower half of the filum terminale consists only of an artery, a vein, and some fibres which represent the atrophied second (and possibly the third and fourth) coccygeal nerve.

As already noticed, the relation which the grey and the white matter bear to one another in amount changes considerably from the cervical region to the conus medullaris. Although there are individual differences, it is as well to tabulate the average measurements made by *Stilling* in a man twenty-five years old.

At the Level of the Attachment of the Lowest Root-fibres of the following Nerves.	CROSS-SECTION IN SQUARE MILLIMETERS.			Proportion of White to Grey.
	Whole Cross-Section.	The White Substance.	The Grey Substance.	
Cervical III, . . .	84.15	71.40	12.73	5.6
" IV, . . .	85.55	72.82	12.73	5.7
" VI, . . .	91.55	74.23	17.32	4.3
" VIII, . . .	78.12	62.92	15.20	4.1
Dorsal I, . . .	65.39	53.73	11.66	4.6
" IV, . . .	57.67	50.26	7.42	6.8
" IX, . . .	42.07	33.94	8.13	4.2
" XII, . . .	52.32	41.71	10.61	3.9
Lumbar II, . . .	57.62	41.01	16.61	2.5
" V, . . .	62.57	39.24	23.33	1.7
Sacral I, . . .	51.96	28.63	23.33	1.2
" III, . . .	22.27	9.45	12.73	0.74
" V, . . .	9.54	4.94	4.60	1.07*
Coccygeal, . . .	4.94	2.47	2.47	1.00*



It must be remarked that in *Stillings's* last five tables of measurements compiled from observations upon other subjects, the white substance from the third sacral nerve downwards, almost without exception, falls below the grey in amount, the slight excess of white matter in the conus medullaris (\*) of this case must therefore be regarded as unusual.

Our knowledge of the spinal cord in different vertebrate animals, though extensive, is as yet incomplete. To *Kölliker's* indefatigable industry we owe the best compendium of data already determined as well as a vast amount of fresh information (*Handbuch der Gewebelehre*, 6th ed.).

## 2. HISTOLOGY OF THE SPINAL CORD.

The sections of the cord which have already served for the study of the more conspicuous variations in structure at different levels may now be used for work with higher powers.

Beginning with the **white sheath** we find that it appears at first sight to consist almost exclusively of longitudinal fibres. In cross-sections, stained in carmine, they 'look like little suns' (fig. 110). The diameter of the fibres, exclusive of the sheath of Schwann, varies; in man from 1·5 to 25  $\mu$ ; in the horse they may be as large as 50  $\mu$ ; in the spinal cords of some fish particular fibres are even larger. Such is the colossal Mauthner's fibre, found in the anterior column of the spinal cord in front of and to the outer side of the central canal in the pike and other fishes, which measures more than 0·1 millimeter. Nearly everywhere thick and thin fibres are mixed together; but certain local peculiarities in grouping are

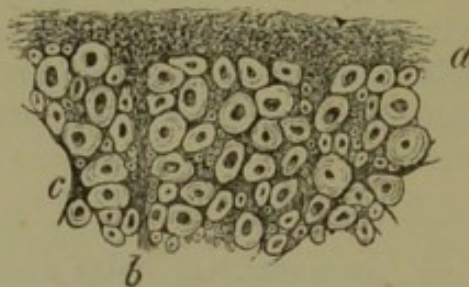


Fig. 110.—Cross-section of the anterior column of the spinal cord. *Stained with carmine.* *Magn.* 150.—*a*, Peripheral grey investment; *b*, a small septum. In the white substance besides the nerve-fibres cut across, some of which are coarse and others fine, three distinct stellate neuroglial cells are seen; one of these is indicated by the letter *c*.

to be noticed. Many thick fibres occupy the peripheral region of the anterior and lateral columns; in the angle between anterior and posterior horns (the central part of the lateral column) thin fibres preponderate. In the posterior column, Burdach's column contains not a few coarse fibres, while Goll's column is entirely made up of fairly fine fibres. The difference between these two subdivisions of the posterior column is especially pronounced in the cervical cord. The larger the fibres which it contains the lighter does any particular region appear when stained with carmine; the smaller its fibres the darker its colour, especially when looked at with



the naked eye or a simple lens. Goll's column, for instance, is in the cervical cord conspicuously darker than its neighbour.

Silver preparations of the embryonic cord show that many of these fibres give off collaterals which penetrate the grey substance to a varying depth, and then break up into arborescent systems. It is quite possible that Ranvier's nodes may be situate at the points of the main fibre from which the collaterals start (*Donaldson*). These collaterals are invested with a medullary sheath, and are often perceptibly finer than the parent fibre. They usually start at an angle, more or less acute, and pass into the transverse plane of the cord (fig. 111).

The fibre is often somewhat thicker at the point of junction than elsewhere. The largest number of collaterals are found in the region of the entrance of the posterior roots, near the posterior horn, and, generally speaking, in the inner zones of the medullary substance. The pyramidal tracts possess but few collaterals, and *Lenhossèk* could discover none in Goll's column and the peripheral layers of the lateral column. The collaterals are not brought out in equal numbers or with corresponding distinctness by many of the methods of colouring at present employed upon the developed nervous system, although the axis-cylinders are very sharply differentiated by some, such as carmine-staining and *v. Gieson's* method. It has, therefore, yet to be proved that their disposition is the same in the nervous system of the adult and the embryo.

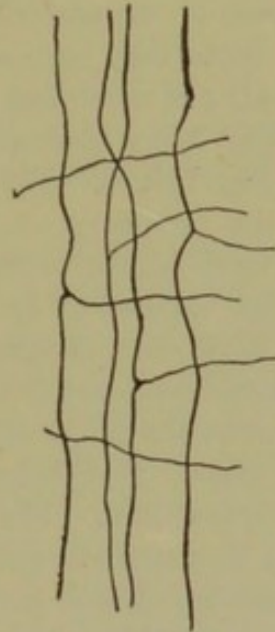


Fig. 111. — Longitudinal fibres with collaterals, from the spinal cord of a human embryo. Silver prep.

In rare instances nerve-cells are found scattered singly in the medulla of the spinal cord.

The periphery of the medullary substance is separated from the pia mater by a thin layer of grey matter, 5 to 40  $\mu$ , or exceptionally as much as 100  $\mu$  thick. This is the cortical layer of the cord, the subpia of *Waldeyer*, the peridyma of *Lenhossèk* (fig. 110, *a*).

The cortical layer is entirely composed of gleia, the fibres uniting in a close felt-work. The cells are not very numerous but rich in processes. Of these, the greater part take a circular course; others, running some longitudinally, some horizontally, either plunge into the white substance of the cord or proceed towards the periphery, where they usually end in a little swelling. There are other gleia-cells lying immediately beneath the cortex or even deeper in the medulla which bear a part in its formation. The little swellings at the end of all the radial fibres which reach the surface unite to form an exceedingly delicate and apparently continuous membrane, the cuticula, or membrana limitans (*His*), or endothelial membrane (*Gierke*) which adheres closely to the inner surface of the pia mater



*Lenhossèk* is of opinion that even if a cleft traversed by fibres should appear in sections between the pia mater and the peripheral layer of gleia, it ought to be attributed to the shrinkage of the preparation consequent upon the hardening process. From the cortical layer septa, some thicker, some thinner, pass through the white substance, carrying numerous vessels with them. They split the white matter into columns, divided again, by lateral septal plates, into fasciculi. The septa themselves are formed of gleia-cells of the cortical layer, the peripheral parts of the grey substance, and cells situate in the septum.

The largest and most constant of these septa, the septum medianum posterius, occupies a place apart. Even in the adult it consists chiefly of processes of the posterior ependyma cells. The forked cleft which in most other septa may be observed, widening by degrees from the periphery to the centre, is much less commonly met with in it.

Many large gleia-cells are interposed between the fibres outside the septa (fig. 110, *c*). They are all long-rayed (see p. 166). Those which lie near the periphery send out numerous processes into the cortical layer, while most of the processes of the inner cells are longitudinally disposed (fig. 72). Hence in transverse sections stained in carmine we see many small dark dots of which it is hardly possible to say whether they are naked axis-cylinders or processes of gleia-cells.

Besides the longitudinal fibres, numerous transverse bundles, as well as fibres, which run obliquely, are also to be found in the medullary substance of the spinal cord. They are:—

(1) The anterior root-bundles which in the cervical and lumbar regions are made up almost exclusively of thick fibres, but contain in the dorsal region many thin fibres also (*Siemerling*). The former are the motor fibres (18 to 20  $\mu$ ) of the skeletal muscles, the latter (2 to 3  $\mu$ ) probably innervate the muscles of the viscera and blood-vessels.

With a view to writing the anatomy of the sympathetic system, *Gaskell* has made transverse sections of all nerve-roots attached to the cerebro-spinal axis in the dog, and, as *Schwalbe* had done for Man, determined the situations in which the small nerve-fibres occur. The ramus visceralis consists of small medullated fibres which enter into the formation of both anterior and posterior roots. It appears that their outflow occurs in the facial and glosso-pharyngeal nerves; for the thoracic region, and to a certain extent also for the stomach, in the vagus nerve; some of the fibres (accelerator, for the heart, and fibres for the abdominal viscera, leave the spinal cord from the second dorsal to the second lumbar nerves, whilst the dilator fibres for the pelvic viscera accompany the roots of the second and third sacral.

No small fibres are found in the roots of the cervical or lower lumbar and first sacral nerves. The series of visceral roots is interrupted in these two regions.

[According to the manner of their peripheral distribution, the visceral fibres may be divided into two groups—(A) those connected with distributive cells in the ganglia which lie nearest to the vertebral column, the 'lateral ganglia' or ganglia of the 'sympathetic chain,' as it is usually called in human anatomy; (B) those which retain their medullary sheaths as



far as the ganglia which lie in the course of the larger blood-vessels, the 'collateral ganglia,' and only by the intervention of the cells of these ganglia are broken up into bunches of non-medullated fibres. These two sets of fibres are differently distributed throughout the three regions of the cerebro-spinal axis to which visceral roots are attached. Class B, or fibres which pass by the lateral ganglia without using their myelin-sheaths, are found in all three regions. Class A is further divisible into the motor fibres for the alimentary canal which leave the cerebro-spinal axis in the vagus nerve, the motor fibres for the walls of the blood-vessels which are entirely restricted to the thoracic outflow, and some others. It appears that the two classes, A and B, are as widely distinct in function as in anatomical disposition. Class A includes motor, accelerator, constrictor fibres, fibres for circular muscles, all katabolic or exhaustive in action. Class B comprises the inhibitory, retarding, dilator nerves, nerves supplying longitudinal muscle-fibres, or in other words, all the visceral fibres possessing an anabolic or restorative function.]

(2) The posterior roots and their collaterals containing thick and thin fibres.

(3) The white commissure which lies at the bottom of the anterior longitudinal fissure, and attains to a thickness of nearly half a millimeter. In most mammals the white commissure does not form a single bundle (or as it may better be described, having regard to its continuity, a compact nervous membrane), as it does in man, but it is made up of many little bundles which cross the anterior fissure at different levels, and pierce the anterior columns instead of lying completely beneath them.

(4) Finally, numerous fibres, singly or in small bundles, traverse the white columns and plunge into the central grey mass, particularly into the anterior horn. These are either longitudinal fibres from the white substance which bend over on the transverse surface, or the collaterals of such fibres.

In the **central grey mass** two substances are to be distinguished, as already mentioned:—A. **Substantia spongiosa.** The grey substance also possesses a gleial scaffolding, the cells of which stain distinctly blue with alum-hæmatoxylin. Here, again, we must turn to the silver method for further disclosures. *Lenhossék* has demonstrated that both long-rayed and short-rayed cells are to be found in the grey horns, the former being especially abundant in the neighbourhood of the large cells of the anterior horn. Among the long-rayed cells those which occupy in large numbers the marginal portions of the grey substance deserve special mention. Their distinguishing characteristic is the fan-like radiation of their processes, which arise almost without exception on the inner side and plunge into the grey substance, hemming it in with a close felt-work.

In successful carmine preparations (especially if alcohol has not been used to harden them), but still better, in sections stained after Weigert's method, the spongy substance is seen to be traversed in all directions by medullated nerves of the most varied calibre (figs. 112, 113). They interlace in all directions, and appear in transverse sections of the cord, cut obliquely and transversely as well as exposed in length. In many places, however, they follow defined directions, as may be pointed out in the following regions:—



The anterior root-fibres are seen to diverge shortly before plunging into the real grey matter of the anterior horn. Within the grey matter they spread out in a broad brush (fig. 112, *a*), both brain- and caudal-wards, as can be seen in sagittal longitudinal sections. The outermost fibres on either side may diverge so far that they form a fibrous layer between the grey and white substance. Other bundles, also running parallel to the transverse section of the cord, are often met with in the marginal portion of the anterior horns, which they to a certain extent encompass. They can be most clearly seen on the lateral margin, particularly in the deep angle made by the junction of the anterior with the lateral horn (fig. 113).

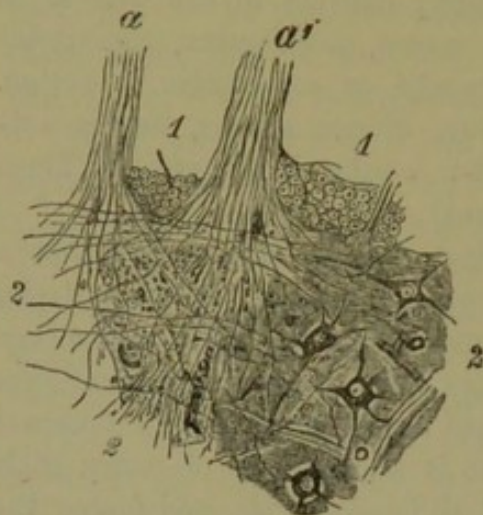


Fig. 112.—Junction of the anterior root-bundles with the anterior horn. Lumbar region. *Magn.* 30.—1, Anterior white column; 2, anterior horn; *a*, *a'*, two root-bundles. On the right side four cells belonging to a group of nerve-cells are to be seen.

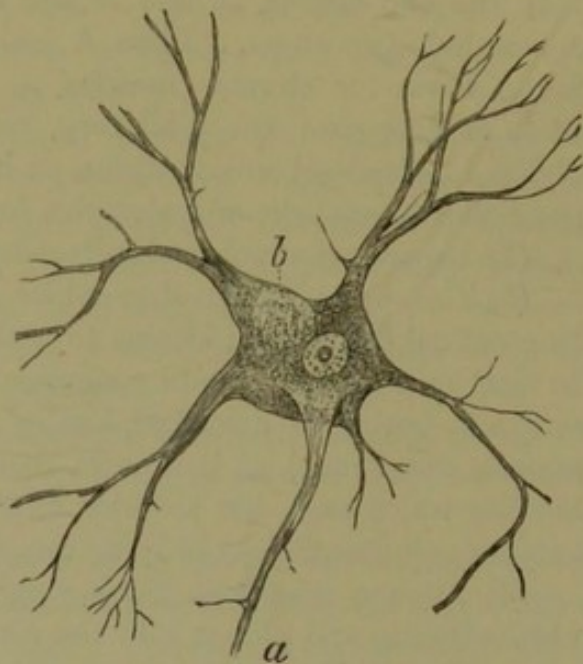


Fig. 114.—A nerve-cell from the anterior horn of the human spinal cord.—*a*, Axis-cylinder process; *b*, clump of pigment-granules.

A conspicuous bundle of thick fibres is often found running backwards from either anterior or lateral horn (*Pal*).

In the anterior horn bundles of fibres are seen to converge towards the white commissure.

The arched fibres of the posterior roots retain their independence far into the substance of the posterior horn. The ground-substance of Clarke's column, as well as the grey matter enclosed within the concavity of the substantia Rolandi (the posterior zone of the substantia spongiosa of the posterior horn), is conspicuous by its clearness in carmine preparations and by its uniform grey colour in those made by Weigert's or Pal's method. It is made up chiefly of a vast number of delicate medullated fibres. In the posterior horn these fibres have for the most part a longitudinal course. Very distinct bundles of coarse fibres also are almost invariably met with running longitudinally. They are in intimate relation with the cells of Clarke's column.

Besides the plexus of medullated fibres the grey substance contains a second network of non-medullated fibres. It is difficult to bring this



second plexus into view in carmine preparations, only occasional fibres being visible. Their cross-sections appear as fine dark dots. By the silver method, however, we can clearly see that this felt-work is made up of the ramifications of arborescent systems and protoplasmic processes.

There are several kinds of *nerve-cell* in the spinal cord. We will begin by considering them as they appear in carmine preparations. The cells of the anterior horn are the most conspicuous (fig. 114). These are frequently



Fig. 113.—Cross-section through the lumbar cord (human). *Pal's staining.* *Magn. 12.*

termed motor cells, since it is generally understood that they give origin to the fibres of the anterior root. These large cells are not limited to the anterior horn, however, for they are found singly in other places, such as the processus reticularis. They have a number of processes (from five to eight), giving them in cross-section a stellate form. In size they vary from 35 to 100  $\mu$ . Methylene-blue staining shows that the characteristic structure of these cells exhibits in its details the type represented in fig. 54. Each cell possesses a large round nucleus, as much as



18  $\mu$  in diameter, with distinct nuclear bodies and nucleolus. They always contain a clump of yellow pigment. Since their processes taper off from the cell-substance it is not possible to define sharply the limits between processes and body, and, hence, various estimates of size are given. The size of the cells is supposed by *Pierret* to bear a direct relation to the length of the fibres to which they give origin. Hence, they are largest in the lumbar swelling—somewhat smaller in the cervical swelling, and smallest in the dorsal region. The axis-cylinder-process of these cells can be sometimes followed for a great distance, usually into an anterior root-bundle, but not rarely also into a fibre-bundle which enters the lateral column (fig. 117). It may be that this difference in course implies a corresponding difference in the functional meaning of the cell. I shall touch upon this point more in detail presently. It has already



Fig. 115.—A nerve-cell from Clarke's column as seen in a longitudinal section of the spinal cord of the horse. *Magn.* 150. The arrow points towards the brain.

been mentioned that, especially in the lumbar enlargement, the cells are collected into roundish groups isolated by grey matter which stains more deeply (fig. 112). The darker colouring is due to the smaller number of medullated, and the greater quantity of non-medullated fibres, as well as to the greater richness in vessels. Each cell is more or less distinctly surrounded by a pericellular space.

The **cells of Clarke's column** are somewhat smaller, 30 to 60  $\mu$  [in transverse diameter], less well provided with processes, and richer in pigment (fig. 115). They are slightly more elongated in their longitudinal than they are in the transverse axis. One or two processes leave the sides of the cell, and almost constantly a single process is attached to either pole. They join the cell more abruptly than the processes of the cells of the anterior and lateral horns, and hence the cell presents a rounder form. Longitudinal sections show us that the pigment hardly ever lies to the side of the nucleus, but is almost always accumulated at one of the poles. Their nuclei are large and conspicuous like those of the cells of the anterior horn. Their processes can often be followed a long distance in longitudinal sections without being seen to divide.

Cells of another kind, presenting every transitional form from those of the anterior horn, are scattered through the spongy substance. They are smaller in size (even as little as 15  $\mu$  in diameter), and have fewer processes; appearing, therefore, triangular or spindle-shaped. Attention should be especially directed to certain stand-points with regard to them.

(1) In the centre of the grey matter lying between the lateral horn and the grey commissure spindle-shaped cells are disposed with a process directed



dorso-laterally towards the arched fibres of the posterior root, of the fibres of the mesial portion of which they may be looked upon as the probable source. Other medium-sized cells are found in this region; *Waldeyer* classes them together under the name of middle cells.

[Other connections for the spindle-shaped cells at the base of the posterior horn have been suggested. *Gaskell* thinks it possible that they give origin to the motor-fibres of the muscles of the alimentary canal, the inhibitory fibres coming, as he may almost be said to have proved, from the cells of *Clarke's* column. The *translator* has on several occasions pointed out that every nerve-fibre is a process of a nerve-cell; that it grows out from the cell in the direction in which it afterwards conducts impulses; that when the fibre has a considerable calibre and traject, a large cell is needed for its nutrition. If these positions can be maintained, it follows that anatomists have been in error in assigning all the conspicuous cells of the spinal cord to extrinsic nerves; the fibres connecting the spinal cord with the brain must start from cells sufficiently large (an unknown relation) to provide for their nutrition. The assumption that the fusiform cells at the base of the posterior horn are connected directly with the fibres of the posterior roots is contrary to the observed course of their axis-cylinder processes (*Gerlach*), and still more opposed to the experimental evidence derived from cutting the spinal nerves, which shows that sensory fibres have their nutrient cells in the spinal ganglia, or in some cases still nearer the periphery, but *not* in the spinal cord. The *translator* thinks it probable that, amongst others, the scattered cells beneath the substantia gelatinosa *Rolandi* bear the same relation to the ascending intrinsic fibres as the pyramidal cells of the cerebral cortex bear to the descending fibres of the pyramidal tract.]\*

(2) At the apex of the lateral horn throughout the whole dorsal cord, and the neighbouring parts of the cervical and lumbar regions, a column of small closely-packed cells, most of them fusiform, is found sharply marked off from the larger motor cells which the lateral horn also contains.

\* For the sake of clearness the above statements are made without qualification, but certain facts with which they seem at the moment irreconcilable are not overlooked. With regard to the assumption that fibres grow in the direction in which they subsequently conduct impulses:—in the case of the motor roots of the peripheral nerves this is obviously true, and much might be said *a priori* in favour of the probability of its being the universal rule. The fibres starting in the olfactory bulb, the retina and the nerve-cells of the lamina spiralis of the cochlea grow inwards towards the cerebro-spinal axis; in other sensory nerves the law, if it be a law, clearly does not apply. The posterior roots of the spinal nerves grow from the cells of the spinal ganglia in opposite directions, one process towards the centre, the other towards the periphery. There may, however, be a morphological reason for this which will reduce it to the level of a further adaptation rather than an exception. If, as there are reasons for thinking, the original sense-organs were situate in the locality of the present spinal ganglia, whether in their present situation or farther afield matters little, and if these organs were, at this time, the only end-stations of sensory nerves, it follows that the extension of sensibility to the surface generally was due to a circumferential growth of the sensory nerves. After the loss of the sense-organs associated with the spinal ganglia, the circumferential growth of sensory nerves still in all probability bears testimony to their mode of origin.



(3) Amongst the scattered cells of the substantia spongiosa, those which lie in various parts of the posterior horn deserve attention.

The behaviour of the cell-processes can be observed in fuller detail by the use of the silver method.

This enables us first to divide the cells into two classes:

(a) Those of which the axis-cylinder process passes out of the grey substance.

(b) Those of which the axis-cylinder process breaks up within the grey substance.

Again, we can subdivide the first class into:

(1) Cells of which the axis-cylinder process enters a nerve-root; and

(2) Cells of which the axis-cylinder process becomes a longitudinal fibre of the white substance.

The cells in the first of these subordinate groups may be called root-cells (*cellules radiculaires*). The best-known of them are the scattered cells found throughout the anterior horn. The chief process of every one of these passes either directly or by a slight circuit into an anterior root and becomes an anterior root-fibre (fig. 116, *a, b, c, d, e*). These fibres sometimes, though rarely, give off collaterals, which run backwards into the grey substance between the cells of the anterior horn. Sometimes, though much less frequently, the axis-cylinder process of a root-cell can be followed to a posterior root (*g*). Most cells of this sort lie in the dorsal part of the anterior horn (*vide supra*).

The protoplasmic processes of root-cells can often be followed for a long distance; some of them cross the middle line behind the white commissure and extend far into the anterior horn on the other side (the protoplasmic commissure of *Ramón y Cajal*). Others extend, sometimes, into the white columns. They occasionally traverse the white columns to the very periphery of the cord. This is especially the case with animals low in the scale.

The cells of the second group are called columnar cells (*f, h, i, k, l, n*), because, instead of forming root-fibres, the axis-cylinder processes which arise from them are continued as longitudinal fibres of the white substance, and go to make up the white columns of the spinal cord. In a limited sense the name columnar cell is applied only to a cell from which the axis-cylinder process enters one of the white columns on the same side (usually the lateral, more rarely the anterior, and most rarely the posterior column) with or without collaterals. In the lateral column the fibre turns upwards (or, less frequently, downwards) almost at a right angle, or divides into an ascending and a descending ramus. When the axis-cylinder process enters the white commissure and is continued as a longitudinal fibre of the anterior column of the farther side, the cell is called a commissural cell.

Finally, there are cells of which the axis-cylinder process divides in the grey substance into several branches, which pass into the various columns of one side or of both. These are the pluricordonal cells of *Ramón y Cajal*.



The cells which fall under the heading *b*, that is, those of which the axis-cylinder process breaks up into its final ramifications within the grey substance (*m, o*), are found in the greatest abundance in the posterior horn. They are the so-called Golgi's cells (*m, o*), or intercalary, or reflex cells.

**B. Substantia gelatinosa.**—Two regions histologically distinct are included under this title. The only feature they have in common is that both are poor in medullated fibres, and consequently appear darker than the rest of the grey substance when stained in carmine or nigrosin, and lighter when stained by Weigert's method or Pal's.

The cap of gelatinous substance which covers the posterior horn, the **substantia gelatinosa Rolandi**, often shows a peculiar striation, parallel in direction with the posterior collateral roots, but only partly to be referred to them.

There is hardly any part of the central nervous system which presents so many difficulties to the histologist. The principal conclusion arrived at by recent methods of staining is that the greater part of the substantia gelatinosa Rolandi is not composed of gleia; indeed, gleial cells and fibres are less abundant here than in other parts of the transverse section of the cord. The silver method shows small and isolated nerve-cells (fig. 116, *o*) with the axis-cylinder process directed backwards in every case. It can never be followed far (*Lenhossèk*). It is also possible to discern a fairly thick plexus of exceedingly fine fibres (*Lustig, Kölliker, Lenhossèk*). As, however, the nature of the actual ground substance of this region is still undetermined, recourse has been had to the examination of its embryonic condition. *Vignal, Cornil*, and others, had already pointed out that the substantia Rolandi in the embryo is very rich in little round cells. *Lenhossèk* was able to demonstrate that these are peculiar nerve-cells of the smallest possible size, most of which send out an axis-cylinder process into the lateral column. In post-embryonic life they probably succumb to a retrogressive metamorphosis, a degenerative process of some kind, and blend into an indistinguishable mass. This theory receives confirmation from the investigation of the conus medullaris in adult life. This must be looked upon as a part of the spinal cord which has remained stationary at a low stage of development. In the most caudal sections of the cord the substantia Rolandi is seen to consist chiefly of pale cells and remains of cells, which have survived from the period of foetal life (*Bräutigam*), while the other and more fully developed parts of the cord have perished by the retrogressive metamorphosis already referred to.

The extreme peripheral stratum of the posterior horn is of a different character from the substantia gelatinosa. This layer, which is rich in medulla, has been called the border zone (*Lenhossèk*), the zonal layer (*Waldeyer*), or the spongy zone (*Lissauer*). Here we find single cells, usually elongated (marginal cells), with axis-cylinder processes directed towards the lateral column (fig. 116, *n, 22*). In the lower sacral cord especially, at a level from which all other large cell-elements have disappeared, certain large scattered and often vesicular cells are very conspicuous on the periphery of the posterior horn.



[The complete history of the substantia gelatinosa has yet to be written. This substance is not distinguishable in the earliest stages of the development of the central nervous system, whereas in what might be called the middle period, after the appearance of the fibre-columns which ensheath the grey matter, and especially about the fifth month of intra-uterine life, the cap of gelatinous substance which covers the posterior horn is extremely large and conspicuous owing to its being packed with small nuclei which stain darkly in carmine.

According to *Corning*, the substantia gelatinosa first appears as a local thickening of the inner layer of the grey matter in its dorsal portion. This thickening extends outwards over the posterior horn to the point of entrance of the posterior roots. Finally, it divides into two portions, or rather the greatly developed cap of the posterior horn breaks away from the original formation which lies in the dorsal wall of the central canal. In new-born animals the same authority tells us it consists of two kinds of cells—the first with large clear nuclei and oval or fusiform cell bodies; the second with darkly staining nuclei and indistinguishable cell bodies. The contrast between the cells of these two classes, the one clearly nervous and the other belonging to the neurogleia, is still more marked fifteen days after birth. The nerve-cells do not lose their indifferent character until after the cells of the anterior horn and the grey matter of the posterior horn are differentiated.

If we bear in mind the origin of the sensory ganglia from rudiments laid down beyond the borders of the medullary plate, but caught in between the lips of the plate as it closes into a tube (fig. 2), and consider that the posterior roots grow into the cerebro-spinal axis from the sensory ganglia, we shall see that it is not improbable that the substantia gelatinosa is also formed from this ganglionic rudiment. If this be the case, it belongs not to the medullary plate, but to the ingrowing sensory root, being, in fact, the brush of filaments into which the short posterior root breaks up on entering the cord, together with their small-cell connections and supporting neurogleia. The long extension of root-fibres up the posterior column is ontogenetically and phylogenetically a later development. *His* concluded from his observations that it is formed from immigrant cells, but looked upon these cells as mesoblastic or connective tissue.

The substance of Rolando is supplied by the arteries of the posterior roots, whereas all the rest of the grey matter receives its blood from arteries which dip down into the anterior sulcus. This is a far-reaching distinction, for the arteries of the roots are strictly segmental, whereas the sulcal arteries arise from the common anterior spinal.

The demonstration by the chrome-silver method of the minute cells (granules) of the substantia Rolandi with their axis-cylinder-processes directed towards the lateral column seems to bring the substance into the same category as the gelatinous (molecular) and granular layers of the olfactory bulb and retina; it points to the local origin of the metamers of the central nervous system. The preponderance of the gelatinous substance in foetal life indicates that the primitive cerebro-spinal axis consisted of the nervous



tissue related to the metameric sense-organs and its connection within the metamer with a motor ganglion. The shrinkage of the gelatinous substance as growth advances is the onto-genetic recapitulation of the process of centralisation which has occurred in the vertebrate nervous system. At first each metamer was complete in itself, with its sense-organ, clump of nervous tissue at its base, and motor ganglia. Gradually the afferent fibres were diverted to higher fields, and what might be termed the 'sense-organ nervous system,' which remains peripheral in the cases of the nose and the eye, was dispersed throughout the higher parts of the central grey tube, including its extension upwards in the brain.]

The substantia gelatinosa centralis surrounds the central canal and spreads out a little into the grey commissure.\* It consists of a close felt-work of neurogleia. In the vicinity of the central canal we find more or fewer angular cells which may well be derived from the epithelium. Here, also, we find some gleia-cells of peculiar character. Their processes are remarkably long and strong. They are for the most part arranged concentrically round the central canal and matted into a close felt-work. In front of the central canal some gleia-cells are visible, which send thick fasciculi through the anterior commissure (the spider-cell commissure of Lenhossék).

A description of the **central canal** is best inserted here. Its epithelial lining has already been referred to, but I must add a few observations on the disposition of the epithelial cells and their processes. We have already seen that in the embryo the peripheral processes of most of the epithelial cells extends radially through the nerve-substance to the pia mater. The posterior columns and posterior horns are not traversed by these fibres. In the cat, only the mesial part of the posterior horn is free from them.

The behaviour of the cells on the anterior and posterior margin of the central canal is quite different. The peripheral processes all form concentric arches, open towards the bottom of the fissura anterior, and thus produce a peculiar marking, which in section resembles an onion (the anterior ependyma-wedge of *Retzius*). The posterior cells form a posterior ependyma-wedge, though their processes are less wide apart, and unite, when they have passed the grey commissure, into a compact bundle, directed sagittally, the septum posticum (or raphe posterior of *Waldeyer*).

I have already mentioned that in the higher vertebrates the radial fibres atrophy as growth progresses; but the septum posticum remains as an abiding vestige of this embryonic rudiment. The cross-section of the central canal varies; in the upper cervical region it is irregular, but usually almost square, and sometimes very wide. It begins to be reduced to a narrow cleft about the level of the fifth or sixth cervical nerves. The cleft is placed frontally coinciding in direction with the grey commissure, but often gives off from its centre a dorsal branch. The frontal extension predominates throughout the dorsal region, although this diameter of the canal becomes less and less, until at last it is almost circular in cross-section. In

\* In many cords the central mass of gleia is very strongly developed; in that case it sometimes sends a pointed process dorsalwards, which penetrates some way into the septum medianum posterius.



the lumbar cord the frontal gives way to a sagittal extension; a disposition which is still more marked in the sacral cord and in the conus medullaris, where the canal consists of an open ventral and often of a narrower dorsal portion. Near the filum terminale the canal dilates into a fusiform cavity about one centimeter long, which presents in section the shape of an irregular triangle (ventriculus terminalis, sinus rhomboidalis inferior) [probably not homologous with the large open sinus rhomboidalis of the bird's lumbar cord about to be described]. The canal appears to end blindly in the upper part of the filum terminale. In Man it can be properly studied only in youthful subjects.

The central canal presents important individual variations in form. Only rarely in the human adult is it found to be completely pervious as in the child and in most animals. In the thick cord of the elephant the central canal is extremely narrow, in that of the dolphin hardly a vestige of it remains. In most cases the sides have in places grown together. The caudal part of the cord from the sacral region downwards presents, as a rule, a continuous canal; so does usually the lumbar cord and the cervical cord from the fifth nerve upwards.

The blocking of the central canal is due to the overgrowth of the epithelium which lines it, as well as of the epithelial cells scattered about in the substantia gelatinosa centralis, and the sub-epithelial glial-tissue. When the overgrowth affects portions of the margin of the canal and not the whole of it, it may give rise to septa dividing the canal into several (as many as five it is asserted) parallel canals. This is the cause of the condition described as double or treble central canals.

In birds a space is left on the dorsal side of the central canal, between the diverging columns of the sacral cord, which is known as the sinus rhomboidalis posterior *seu* inferior. It is filled with a gelatinous substance extending in some cases as far as the ventral periphery of the central canal.

### 3. COURSE OF FIBRES IN SPINAL CORD.

Sections from the normal adult human organ are insufficient to reveal the course of fibres in the spinal cord. But little light would have been shed upon the relations of the various fibre-systems, which are by no means simple, without the help of pathological and developmental observations.

Root-fibres, which are the direct continuations within the cord of fibres which form the roots of the spinal nerves, are to be looked upon as of equal value with peripheral nerves; like them they are early covered with myelin, sooner indeed than any portion of the white columns of the cord. The dorsal roots ought not perhaps to be treated unconditionally as peripheral nerves, since some of them have already suffered an interruption to their course in the cells of the spinal ganglia, but yet they belong to them both histologically and histogenetically.

The **anterior roots** (fig. 119; *Ra*, 1, 2, 3, 4, 5, 6) originate without exception from the cells of the anterior horn (fig. 116), the coarser, which



are also the more numerous, from the large cells, the finer from the small ones (*cf.* figs. 52 and 54). Fibres from different sides converge to form a

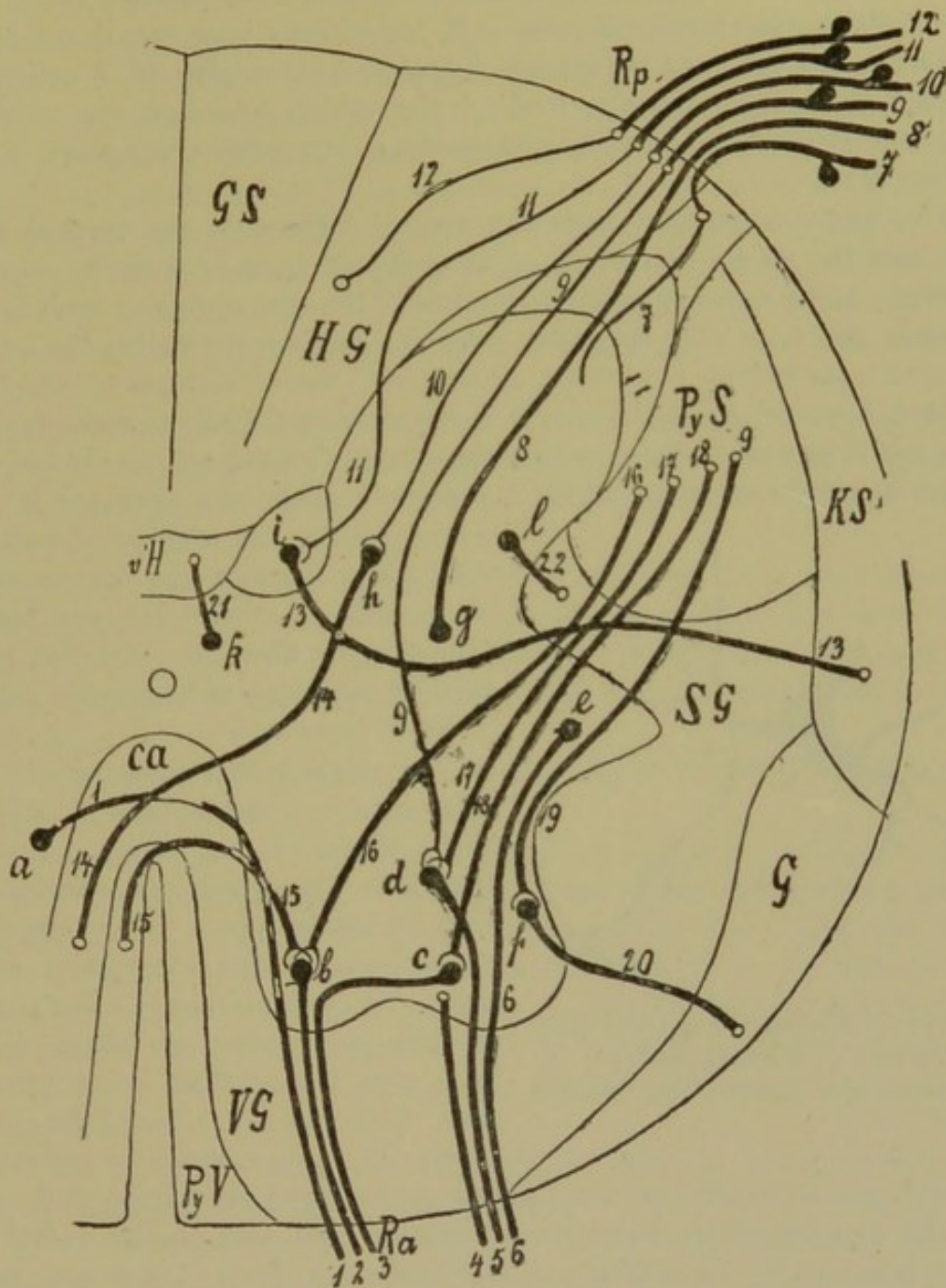


Fig. 116. — Diagram showing the course of fibres in the spinal cord. *B*, Burdach's column; *ca*, anterior commissure; *Cl*, Clarke's column; *G*, Gowers' bundle; *GS*, Goll's column; *KS*, lateral cerebellar tract; *L*, border-zone of Lissauer; *PyS*, lateral pyramidal tract; *PyV*, anterior pyramidal tract; *Ra*, anterior root; *Rp*, posterior root; *SG*, ground-bundle of lateral column; *VG*, ground-bundle of anterior column; *vH*, ventral posterior column-field; *a, b, c, d, e, f, g, h, i*, situation of the several arborescent systems of afferent fibres.

root-bundle, which thus consists of processes of cells lying some distance apart and at different levels in the cord.

Some root-fibres (*1*) originate from the cells (*a*) of the contra-lateral



anterior horn (*Lenhossèk* denies this); and, as the root-fibres are the first to acquire a myelin sheath (which they do in the first half of the fifth month) and the white commissure is otherwise destitute of myelin, these few crossed fibres are easy to discover. It has already been mentioned that, before leaving the grey substance, many root-fibres give off a collateral directed backwards. In the cord of the rabbit *Lenhossèk* was able to discern these collaterals thickly interwoven on the anterior periphery of the anterior horn.

The root-bundles start from the ventral surface (in the cervical cord only from the mesial half of it) of the anterior horn in a curve, concave outwards, and pierce the anterior columns of the cord obliquely from below upwards, the more obliquely the nearer the section approaches the end of the cord. According to *Birge's* calculations, the correctness of which is doubted, however, by *Gad* [for it is obviously very difficult to recognise the same cell in several sections, or to make certain that the cell counted to one section is not the same cell which has already made its appearance in the

section above], the number of cells in the anterior horn (in the frog at least) corresponds exactly to the number of issuing motor-fibres, so that one may consider each fibre as having its origin in one of these cells.

The physiological meaning of the cells of the anterior horn is still a fertile theme of controversy. In the first place, their purely motor functions must be insisted upon. Every impulse which leads to the contraction of a group of muscle-fibres must pass through a number of these cells. True, even this cardinal point cannot pass unchallenged (*Schiff*, for one, denies it). They are also generally

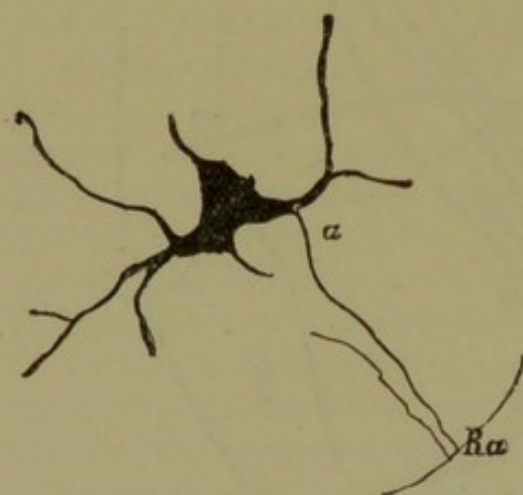


Fig. 117.—Cell from the anterior horn of the cord of a human embryo. *a*, Axis-cylinder process; *Ra*, anterior root.

looked upon as trophic centres for the nerves which start from them, and for the muscles which these nerves supply; but this trophic meaning, again, is denied by many (*Pal* and *Kronthal*, *inter alios*). The reason given for this denial is that the anterior cells of the spinal cord are said to degenerate without necessarily causing the destruction of the nerves which proceed from them to the periphery, while, on the other hand, muscular atrophy has been observed when the cells of the anterior horn were apparently intact; whereas for the motor nerve-fibres issuing from the brain, the law holds good throughout that the maintenance of their normal structure is indissolubly bound up with the integrity of their cells of origin (*Kronthal*). These cells may also possess reflex functions, including that of adjusting the muscle-tone by reflex action.

Vasomotor and sudatory centres should also be sought in the anterior and lateral horns (*Sherrington*).



With regard to the physiological functions of the various motor nerve-roots and cell-groups some general facts should be borne in mind.

In relation to the muscles which it supplies, each nerve-root that leaves the cord is physiologically rather than anatomically a unit. *Ferrier* and *Yeo* have demonstrated that irritation of any motor root in the ape calls forth complicated movements in keeping with the habits of the animal. Thus, irritation of the first dorsal root produces the movement of plucking a fruit; the eighth cervical, the scalptor ani action; the seventh cervical, a movement as if the body were being lifted, the hands clinging to a branch; the sixth cervical, carrying the hand to the mouth. Similar relations exist in man, as can be seen from certain diseases of the roots and plexuses, such as Erb's paralysis, which affects the fifth and sixth cervical nerves.

But, on the other hand, the cell-group which innervates any particular muscle, its nuclear region, often extends into several segments of the cord, and the root-fibres of a single muscle are often distributed through several consecutive roots and root-bundles.

Another great difficulty in the way of determining the position occupied in the spinal cord by the nuclei of origin of single muscles is that we are obliged to rely for our conclusions almost entirely upon localised and isolated diseases of the cord, of which few have hitherto fallen under observation.

The classification proposed by *Collins* would establish the following facts with regard to the cervical cord:—

The cell-groups for the plexus brachialis extend from the upper end of the fourth cervical segment to the lower end of the first dorsal segment, and may be divided into three subordinate groups, the uppermost being destined for the shoulder and upper arm, the lowest for the forearm and hand. The nuclei of the flexor muscles lie deeper and farther to the side than those of the extensor muscles. The cells which innervate the muscles of the back lie inside the ventral part of the anterior horn (or on its mesial border, *Kaiser*).

In the cell-group which extends from the medulla oblongata into the seventh segment, attaining its highest degree of independence in the processus ventralis and medius (p. 209) in the region of the lower cervical cord, *Kaiser* sees the nucleus of the nervus accessorius. *Prevost* and *David* fix upon the lateral group of cells in the lower cervical cord as supplying the thenar muscles. It is possible that the middle group of cells at the level of the fourth and fifth lumbar nerves belong to the calf-muscles (*Kahler* and *Pick*). From a case observed by *Schulze*, it would appear that the nerve-cells belonging to the region of the anterior crural and obturator nerves in Man do not lie in the lowest segments of the lumbar swelling, and *Remak* is of opinion that the musculus tibialis anticus, though supplied by the nervus ischiadicus, has its nucleus near the origin of the cruralis.

From experiments upon rabbits, *v. Sass* concludes that, generally speaking, the muscles situate in the upper part of the extremities in Man have their cells of origin in the upper segments of the anterior horn.



*Lehmann* places the motor cell-groups for the quadriceps muscle in the rabbit between the point of exit of the fifth, sixth, and seventh lumbar nerves.

The centres for the innervation of the bladder and rectum must be looked for in the upper sacral cord.

The intra-medullary course of the posterior root-fibres is much harder to determine with certainty.

We must not forget that a small proportion of them (fig. 116, 8) end in cells in the spinal cord (*g*), and therefore, in all likelihood, do not conduct centripetally. This connection is particularly well seen in the cord of *Petromyzon* (*Frewl*) [although its meaning is doubtful, for we must bear in

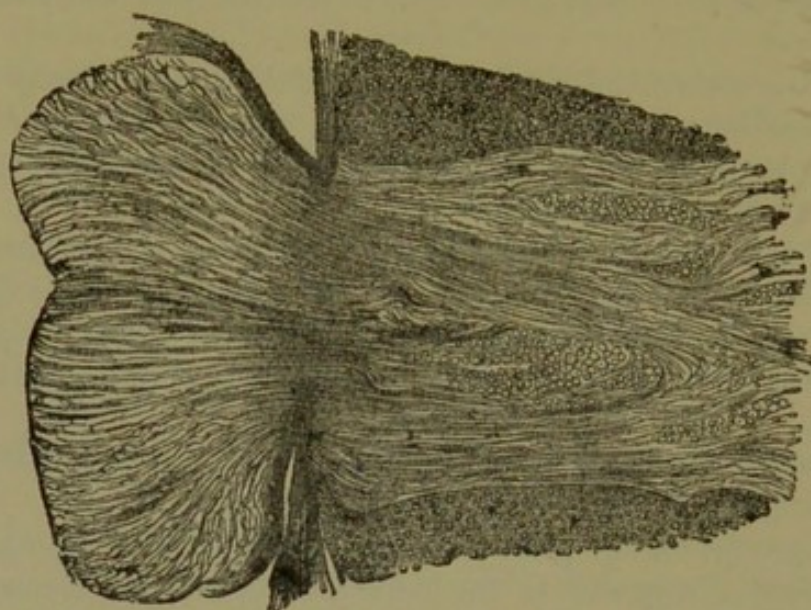


Fig. 118.—A normal posterior root from the lumbar cord at its entrance into the cord. *Nigrosin-staining*. The root looks darker at the point where it is strongly constricted by the pia mater, owing to the attenuation or absence of the medullary sheath.

mind that the constitution of the posterior root in *Petromyzon* is different to that of mammals (*D'Arcy Thompson, Ransom*)]. But by far the greater number of the fibres which compose the posterior roots represent axis-cylinder processes of cells of the spinal ganglia. On the other hand, the number of cells in the spinal ganglia is from five to six times as large as that of the posterior roots belonging to them (*Lewin, Bühler*). Again, the number of nerve-fibres peripheral to the ganglion exceeds the combined total of the posterior and anterior roots by from 19 to 25 per cent. We must therefore ascribe a more complicated meaning to the spinal ganglia. The root approaches the spinal cord in the sulcus lateralis posterior as a compact bundle. At the point where it pierces the pia mater and the cortical layer it is constricted, sometimes to a very marked extent (fig. 118), though the degree of constriction varies in different subjects. This reduction in size takes place entirely at the expense of the myelin sheath. Consequently, it may happen that, when stained by Weigert's method, the root remains colourless at this point, while the extra-medullary and intra-



medullary portion turn quite black. In this case a bright band, usually a little convex on the outer side, is seen traversing the root at the point of constriction.

In the posterior roots thin fibres everywhere accompany thick ones. Outside the point of constriction just described, the finest fibres (fig. 116, 7) are generally collected on the periphery of the root, with the exception of its mesial part. In Weigert-preparations we see that within the cord they immediately enter a transverse field (*L*) situate between the tip of the posterior horn and the periphery, and, conspicuous from its light grey colour, the boundary zone of *Lissauer*, medullary bridge of *Waldeyer*, posterior lateral root-zone of *Flechsig*. They are medullated later than the mesial root-bundles.

The thicker mesial root-fibres divide again into a lateral and a mesial group. In carmine- or Weigert-preparations the fibres of the former (8, 9, 10) seem to penetrate the substantia gelatinosa, traverse it in many slender bundles, and reach the inner part of the posterior horn. The mesial bundles (11, 12) appear to pierce Burdach's column in wider or closer curves. A part of them seem to stream into the ventral part of the posterior horn. But no single arched fibre can be followed without a break from its entrance into the cord to the grey substance. It was therefore supposed that these root-bundles turned longitudinally soon after entering Burdach's column and ran for some way in that direction before resuming their former horizontal course.

Momentous discoveries recently made (notably by *Ramón y Cajal*, *Golgi*, *Kölliker*, and *Lenhossék*) have given an entirely new interpretation to this circumstance and to the whole behaviour of the posterior roots within the cord.

The application of the silver method to embryonic cords makes it plain that all—or almost all—posterior root-fibres divide soon after entering the medulla of the cord into two branches, forming a Y, of which one limb runs up and the other down, so constituting (at least in part) the posterior columns. From both of these longitudinal fibres (stem-fibres) collaterals (sensory) go off at right angles, especially in the earlier part of their course. These run horizontally into the grey substance, and, like the longitudinal fibres themselves, break up into arborescent systems. The results of observations made on the embryos of animals cannot, of course, be immediately transferred to adult human beings, but *Lenhossék* and *Kölliker* have found a similar state of things in the human embryo. *Ramón y Cajal* succeeded in exhibiting this bifurcation in full-grown specimens of frogs and small mammals. There is invariably a Ranvier's node at the point where it occurs. Not seldom a strong collateral starts from the angle thus formed. It may be taken for granted that the course of the descending branch is short, and that the ascending branch, after a course of varying length, bends round into the grey substance. In many cases it extends to the beginning of the medulla oblongata. The fibres which are continued upwards constitute Burdach's and Goll's columns. Single root-bundles of coarse fibres seem to take a longitudinal inclination only after entering the



posterior horn; they can be easily distinguished in the cross-section as the longitudinal bundles of the posterior horn, or Clarke's ascending columns.

With regard to the course and end of the sensory collaterals, the following facts may be taken as proved:—Their final ramifications spread through the whole cross-section of the grey substance on the same side and across into that of the other side (*Lenhossék*), and thus come into relation with most of the cell-groups, the lateral and mesial root-bundles exhibiting in this connection differences of behaviour. The felt-work into which they finally break up seems to be closest in the substantia spongiosa of the posterior horn (nucleus of the posterior horn), where collaterals from the boundary zone of *Lissauer* meet others which have traversed the substantia Rolandi or Burdach's column. A large number of the arched collaterals which pass through Burdach's column (11) reach the cells of Clarke's column (*i*), and wrap them round with a close network of arborescent processes. In this basal region of the posterior horn a considerable body of collaterals can be seen collected into a conspicuous bundle (9), from which they radiate, fan-like, into the anterior horn, and doubtless come into relation with its motor cells (*d*).

Fig. 119. — Diagrammatic representation of the course of the posterior root-fibres. *p*, Peripheral sensory nerve-fibres; *g*, cell of the spinal ganglia; *r*, root-fibre, dividing into *a*, the ascending, and *d*, the descending branch; each with its collaterals and arborescent process.

This bundle, which is present in Man, and particularly well marked in some animals, is the sensory-motor bundle (*Ramón y Cajal*), or antero-posterior, or dorso-ventral reflex-bundle. *Pal* is of opinion that this bundle contains posterior root-fibres which pass into the anterior column. Some collaterals (10) are said to fix themselves on to the cells of the commissure, *h* (*Edinger*), which send their axis-cylinder processes (14) into the contralateral antero-lateral column. Other sensory collaterals from the boundary zone (though in Man only a few) are said to extend to the posterior commissure, and break up into their end-ramifications in the posterior horn of the other side. That they can only be few is proved by the fact that in *tabes dorsalis* the posterior commissure contains a fair number of sound fibres, while the intra-medullary parts of the posterior roots elsewhere are completely degenerated. *Loewenthal* has demonstrated that many posterior root-fibres (stem-fibres probably, not collaterals) pass through the posterior commissure and extend into the contra-lateral posterior column. Since, however, the total area of the cross-section greatly exceeds that of the



posterior columns, we may take for granted that the fibres which bend round into the grey substance are not all collaterals, but that stem-fibres also leave the column in this manner.

From what has been said, it will readily be understood that the fibres of which the posterior roots are composed are by no means all of equal value; this is further proved by the fact that they develop in at least four or five successive groups (*Flechsig*). We must, therefore, assume that the diverse anatomical relations of the fibres of the posterior roots answer to differences in function.

But little, however, can be alleged in this connection; the fibres which run brainwards in Goll's column may conduct sensations from the muscles; while the cells of Clarke's column are, perhaps, the halting-stations on the roads along which the visceral sensations travel. Sensations of pain, heat, and cold must probably pass through the grey substance of the posterior horns. Both experiment and clinical observation of unilateral lesions of the cord, causing motor paralysis of the same side, and anæsthesia of the skin on the other side below the seat of the injury (Brown-Séquard's paralysis), have led us to the conclusion that the little-known tracts which conduct sensation from the skin, cross slightly above the point at which they enter the cord. Anatomists have not yet discovered the locality of the crossing. The posterior commissure is certainly too poor in fibres; and we should rather expect to find it brought about in the anterior commissure by the agency of the commissural cells (*Edinger*). But the Brown-Séquard theory of hemianæsthesia stands in need of serious modification.

The numerous collaterals go to prove that, in the case of tracts in the spinal cord, a sharp definition of conducting-paths, in the old sense of the word, cannot be insisted on. But we have as yet no clear idea of the conditions of transference of impulse.

With regard to the meaning of the individual posterior roots, we know several facts; as, for instance, that those which enter at the junction of the lumbar and dorsal segments contain the fibres chiefly concerned in causing knee-jerks (*Westphal*).

In any case, a relation corresponding to that of the anterior roots to the muscle-groups must exist between the posterior roots and the sensitive parts which they supply; and from this we may infer a principal connection between certain segments of the cord and certain parts of the skin; though it must be of a somewhat different sort from that relation which subsists between the motor nerves and the muscles which they innervate, since the motor nerves spring directly from the cord in the segments in question. We may assume that every part of the skin is innervated by several sensory roots (two or three).

[In recent years evidence has been rapidly increasing in proof that disease of the spinal ganglia, without primary disease in the grey matter, gives rise to ascending degenerations. So, too, on the experimental side it is found that severance of posterior roots produces tracts of degeneration which ascend for a short distance in the postero-external column, and then in the postero-internal column, for the whole length of the cord. Probably the



degenerated tract dwindles as it passes upward, showing that its fibres were not all of them destined for regions above the cord. By careful severance of particular roots, the location in Goll's column of the tracts associated with the several sensory nerves can be accurately determined. It is found that the fibres from the sacral region of the cord occupy, in the dorsal region, a small tract, triangular in section, the triangle being bounded by the posterior fissure on one side and the periphery of the cord on the other. Lumbar fibres are applied to the outer side of these and nearer the central canal; dorsal fibres still deeper, and more external in the cord. Cervical fibres form, apparently, a more extended sheet, which extends from the grey commissure to the periphery.

Everything points to a primitive nervous system of strictly segmental character, each segment comprising a sense-organ, deposited sensory cells serving as ganglionic cells at the base of the sense-organ (the present spinal ganglion), granular and molecular tissue (substantia Rolandi), motor cells (anterior horn). Gradually, as functions became centralised in the bulb and brain, the sensory fibres extended farther and farther up the cerebro-spinal axis; but the primitive metameric reflex paths still remain.]

The **white matter** of the cord is divided into several parts, the boundaries of which have been determined by studying its pathology and development. It must be premised that the number of longitudinal bundles which it is possible to distinguish from one another is constantly being increased by continued observation, and that the differentiation of separate groups of fibres promises to become more and more detailed. Nearly, if not quite all of these divisions comprise fibres of various connections, but in almost every case there is such a preponderance of one kind that the others are apt to be neglected.

A distinction between the long and short tracts in the spinal cord is first to be insisted on. Short tracts unite places in the grey matter which lie near together, while the long tracts consist of fibres which can be followed into the medulla, or even farther. In sections this difference is not demonstrable, but it is brought out in pathological or experimental lesions of the cord. The short tracts show degeneration in the neighbourhood of the injury only, while degenerated bundles in the long tracts can usually be followed brainwards and caudalwards through the whole cord.

In the anterior columns of each side we have to distinguish, at least, four long tracts. The several divisions in the white matter are not, however, the same at all heights, so, first, as a paradigm, we will examine a somewhat schematised transverse section of the cervical cord (fig. 120).

(1.) The anterior pyramidal tract, *PyV* (Türck's bundle), lying on either side the anterior fissure, forms the mesial tract of the anterior column, and very often extends outwards along the free ventral surface of this column. (2.) The lateral pyramidal tract, *PyS*, which in the dorsal region occupies a large part of the lateral column. (3.) The lateral cerebellar tract [direct cerebellar tract], *KS*, a small column, swelling out slightly on the ventral side, lying between the margin of the lateral column and the lateral pyramidal tract. (4.) Gowers' bundle, *G*, lying partly as



a small marginal column on the ventral side of the direct cerebellar tract, partly in the midst of the lateral column on the ventral side of the lateral pyramidal tract.

As short tracts there may be distinguished in the antero-lateral columns of the cervical cord—(1.) The anterior ground bundle, *VG*, the part of the anterior column, that is to say, which remains after allowing for the anterior pyramidal tract. (2.) The tract, *SG*, bounding on the outer side the grey matter of the anterior horn, and filling up the space between

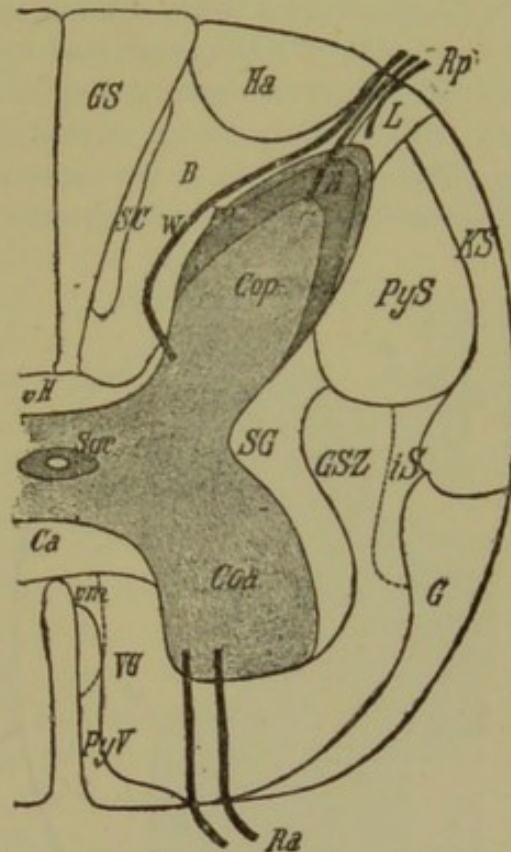


Fig. 120.—Diagrammatic cross-section through the cervical cord; *B*, Burdach's column; *Ca*, anterior commissure; *Coa*, anterior horn; *Cop*, posterior horn; *G*, Gowers' bundle; *GS*, Goll's column; *GSZ*, mixed lateral zone; *Ha*, postero-external tract; *iS*, intermediary bundle of the lateral column; *KS*, lateral cerebellar tract; *L*, border zone of Lissauer; *m*, marginal zone; *PyS*, lateral pyramidal tract; *PyV*, anterior pyramidal tract; *R*, substantia gelatinosa Rolandi; *Ra*, anterior root; *Rp*, posterior root; *SC*, Schultze's comma; *SG*, lateral border tract; *Sge*, substantia gelatinosa centralis; *Vg*, ground-bundle of the anterior column; *vH*, ventral tract of the posterior column; *vm*, fasciculus sulco-marginalis; *W*, root-zone.

the posterior horn and the lateral pyramidal tract, lateral ground-bundle. (3.) The mixed zone, *GSZ*, in the lateral column, which comprehends all that now remains of it, together with the intermediary bundle of the lateral column. *Hellweg* gives the name of 'three-sided tract' to a triangular area which lies laterally to the most lateral of the anterior roots, its base turned dorsalwards, its apex to the periphery. He found that in insane persons it consisted almost entirely of very fine fibres.

Only one long tract situate mesially, Goll's column, *GS*, is with certainty distinguished in the posterior column. To the short tracts belongs in part the ground-bundle of the posterior column, *HG* (the lateral or



Burdach's column). This can be divided into several parts: the root-zone, *W* (zone radicaire), that is, the region through which the posterior roots and their collaterals bend; the posterior external region, *Ha*, occupying the periphery between the entrance of the posterior roots and Goll's column, and standing towards the former in some relation not yet fully understood. The most ventral part of the posterior columns, the ventral posterior column field, *vH*, a peculiar crescent-shaped area bordering on the posterior commissure, must also be regarded as distinct. Further, in the upper half of the cord, between Goll's column and Burdach's, we can distinguish a narrow space, *SC*, the comma-shaped tract of *Schultze*; and between the posterior and lateral columns a longish tract intervenes, the border zone of *Lissauer*, *L* (medullary bridge of *Waldeyer*, lateral posterior root-zone of *Flechsig*), which corresponds to the caput cornu posterioris.

As we approach the caudal end, this arrangement of the various parts

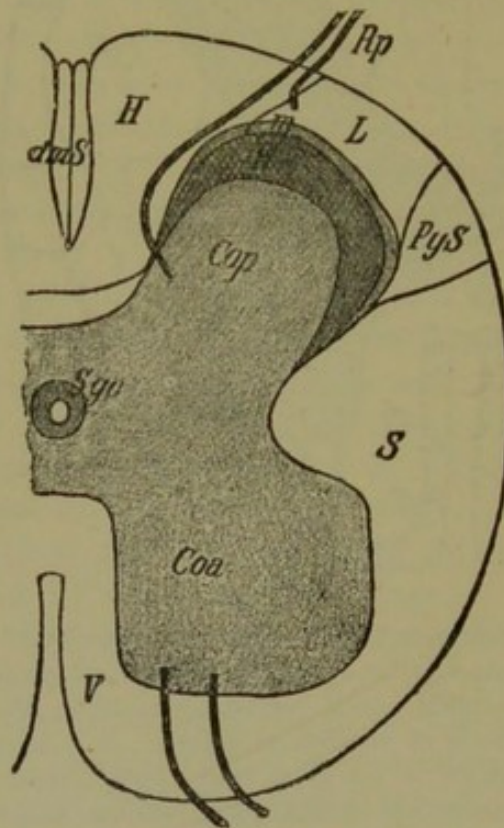


Fig. 121.—Diagrammatic cross-section through the lower lumbar cord. *Coa*, Anterior horn; *Cop*, posterior horn; *dmS*, dorso-mesial sacral bundle; *H*, posterior column; *L*, border zone of Lissauer; *m*, marginal zone; *PyS*, lateral pyramidal tract; *R*, substantia Rolandi; *Rp*, posterior roots; *S*, lateral column; *Sgc*, substantia gelatinosa centralis; *V*, anterior column.

of the cord gradually alters. Fig. 121, a schematised representation of a section through the lower lumbar cord, shows the differences.

The order in which the separate constituents of the white substance of the cord become medullated is as follows:—

- (1.) The anterior and posterior root-fibres. (2.) The ground-bundle of the anterior column. (3.) The ground-bundle of the posterior column.
- (4.) The anterior mixed lateral zone. (5.) The lateral marginal layer. (6.) The lateral cerebellar tract (in the beginning of the sixth month of



foetal life). (7.) The mesial posterior column (end of the sixth month). (8.) Gowers' column, in the eighth month. (9.) The lateral and anterior pyramidal tracts (which in man are first medullated at or after the time of birth).

It must, however, be noted that all the fibres of any one tract do not acquire the myelin-sheath at the same time; whence we infer a difference in function between those which develop at different periods.

The **pyramidal tracts** are composed exclusively of nerve-fibres arising from cells in the motor region of the cortex cerebri. One set of these fibres, the anterior pyramidal column (fig. 120), *PyV*, runs at first along the same side of the cord, occupying the mesial border of the anterior horn, and often hooking a little way over the anterior periphery. Another set, the lateral pyramidal column, *PyS*, crosses the middle line in the medulla oblongata (the pyramidal crossing), and collects in the posterior half of the lateral column. All these pyramidal fibres probably give off collaterals, which enter the anterior horns. It is also probable that the fibres of the anterior pyramidal column turn dorsally and mesially by degrees, cross the line in the anterior commissure (fig. 116, 15), and arrive at the lateral pyramidal tract, after passing through the grey substance of the anterior horn; or break up within the anterior horn into arborescent processes which attach themselves to the motor cells, *b*. It may be that single fibres reach the motor cells on the same side without crossing; indeed, *Lenhossék* denies the existence of the subsequent crossing of the pyramidal fibres. At all events, the anterior pyramidal tract gradually disperses, and cannot, in most cases, be followed as far as the upper dorsal cord.

The form and situation of the lateral pyramidal tract changes at different heights. Where it is best formed it extends ventrally from the posterior horn, almost to a line carried transversely through the posterior commissure. From the cervical to the sacral cord it exhibits a constant diminution in its cross-section; by the time the lumbar swelling is reached it is reduced to a small layer on the outer side of the caput cornu posterioris (fig. 121). The increase in the lateral pyramidal tract from below upwards (which is especially marked in the swellings) is chiefly due to fibres (16, 17, 18) which stream into the lateral column from the lateral border of the grey horns. The arborescent processes of these fibres afford a connection with the nerve-cells of the grey substance.

The lateral pyramidal tract rests against the grey substance of the posterior horn, and especially against that part which lies nearest to the periphery. It is cut off from the periphery in most places by the lateral cerebellar tract, but reaches it near the apex cornu posterioris from the eleventh or twelfth dorsal nerves downwards, and for a short space in the neighbourhood of the third cervical nerve (*Gowers*). It is club-shaped at first, but becomes triangular when it reaches the lumbar cord.

Descending degeneration in the cord, whether the lesion is situate in the brain or in the cord itself, affects the crossed and direct pyramidal tracts (*PyS* and *PyV*), though not those alone. The degeneration-areas correspond exactly with the developmental areas (fig. 122). In one-sided lesions of the brain which give rise to descending degenerations, it is the direct



pyramidal tract (*PyV*) of the same side, and the crossed pyramidal tract (*PyS*) of the opposite side, which are affected. On close examination, however, it is frequently possible to discover a degeneration, although less marked, in the lateral pyramidal tract of the same side, and, perhaps, even in the anterior pyramidal tract of the opposite side. The degenerated area is considerably larger when the seat of the injury is in the cord than when it is in the brain. This may be because an injury to the brain rarely affects all the pyramidal fibres, or because in transverse lesions of the cord the descending degeneration involves other fibres than those of the pyramids proper, the fasciculus intermedio-lateralis, for example, or the fasciculus sulco-marginalis. It is also supposed that descending fibres from the cerebellum run through the region of the cross-section of the lateral pyramidal tract (*Biedl*). In descending degeneration of this part there are always a number of sound fibres to be found, whence we may fairly conclude that scattered throughout it are a certain number which conduct upwards. Descending degenerations are diffuse in the dog (*Schiefferdecker*). *Marchi* and *Algeri* found scattered degenerations in every part of the cord after injury to the cortex cerebri of the dog; descending degeneration of Burdach's columns was especially conspicuous when the portion of the cortex which they destroyed lay behind the motor zone of the opposite side, which proves that, in the dog at least, a part of the pyramidal tracts must run in the posterior columns; while in most rodents all the pyramidal fibres unite in a compact bundle in the ventral part of the posterior columns on either side (*Stieda*, *Spitzka*, *Lenhossék*). In the guinea-pig they are, indeed, found in the same region, but only as scattered bundles, chiefly in the vicinity of the grey substance (*Bechterew*). In the mouse the pyramidal tracts occupy only 1.14 per cent. of the total cross-section of the middle cervical cord, in the cat 7.76 per cent., and in the human foetus when 36 centimeters long 11.87 per cent. (*Lenhossék*).

In many mammals we find on the mesial and part of the ventral border of the anterior column a region which extends far down into the lumbar cord, and is characterised by descending degeneration of numerous fibres (the 'vorderes Grenzbündel' of *Loewenthal*, the fasciculus sulco-marginalis descendens of *Marie*), while in nearly all animals the anterior pyramidal tract is lacking. The 'anterior boundary-tract' appears also to be present in Man. It degenerates only after injuries to the cord, never after injuries to the brain, and probably contains only fibres which serve to connect the several segments. The fibres which compose it are particularly coarse. It may have a parallel in low classes of vertebrates.

[We do not as yet understand in all respects the course taken by degenerations secondary to destruction of the cortex. An attempt has been made by *Sherrington* to determine the exact number of degenerated fibres found at all levels of the cord, and the situation of these fibres in the cord; and although these observations throw much additional light upon the question of fibre-dependencies of the cortex, the results are in some points still inexplicable. It is found, for example, that a strictly localised destruction of the arm-area in the monkey (or even of the face-area?) gives



rise to the appearance of degenerated fibres throughout the whole cord; while, on the other hand, lesion in the leg-area induces degeneration which in great part stops short in the cervical enlargement. Every unilateral lesion induces degeneration in both lateral pyramidal tracts, the smaller degeneration (on the same side as the lesion) being most pronounced in the cervical and lumbar enlargements, immediately above which regions it is often absent. It follows, therefore, that the degeneration on the same side as the lesion is a 'recrossed' degeneration. Not only may the number of degenerated fibres not decrease regularly from above downwards, but the lower regions may even contain more degenerated fibres than the upper ones. It is obvious, therefore, that fibres branch as they descend in the white columns, and as degenerated fibres can often be traced for a long distance in pairs, it is inferred that the fibres divide into two. These pairs, termed 'geminal'

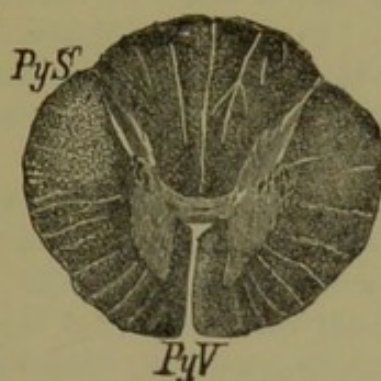


Fig. 122.—Descending degeneration after a one-sided lesion of the brain. Section through the upper part of the spinal cord. The anterior pyramidal tract of one side, and the crossed pyramidal tract of the opposite side, are degenerated. The healthy lateral pyramidal tract shows a somewhat light staining. *Magn. 4.*

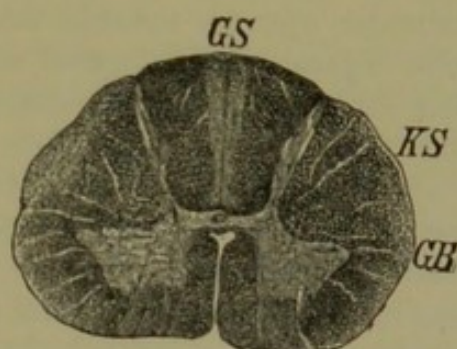


Fig. 123.—Ascending degeneration in the cervical swelling. Goll's column, *GS*, degenerated on both sides; and, to a less degree, the lateral pyramidal tract, *KS*, and Gowers' tract, *GB*. *Magn. 4.*

fibres, are much less frequent in the recrossed than they are in the crossed pyramidal tracts.

*Sherrington* suggests that the pyramidal tracts conduct cortical visceral as well as cortical somatic fibres, and that the degeneration in the lumbar region following lesion in the arm-area may be explained in this way. The conclusion of *François-Franck*, that the disturbances of the vascular and visceral systems which follow stimulation of the cortex in *curarised* animals are true instances of cerebral visceral epilepsy, lends support to the view that visceral and somatic fibres lie side by side in the same tract. This is the only suggestion of which we are aware which attempts to explain the apparent discrepancy between the anatomical tract and its functional import; but the obvious morphological improbability of the same area of the cortex representing muscles of one segment of the body, and vessels or viscera of a different segment, stands in the way of its acceptance. Since so much of our knowledge of the course of fibres is derived from a study of



degenerations, it is very important that we should know the exact causal relation between destroyed grey matter and degenerated white tracts.]

The **lateral cerebellar tract**, *KS*, is not found below the level of origin of the upper lumbar nerves. Ascending from this level through the lower dorsal cord it grows rapidly in cross-section; as it reaches the upper dorsal and lower cervical nerves its increase becomes slower. Its greatest increase in size occurs in the region in which Clarke's column of cells is best developed. The coarse fibres composing it can be followed without crossing up into the surface of the cerebellum. In the upper cervical cord there is often no sharp line of demarcation between the lateral cerebellar tract and the lateral pyramidal tract, the fibres of both being mixed in a region of varying breadth. With lesions of the spinal cord situate above the first lumbar nerves (or after destruction of the posterior roots at a corresponding level, *Edinger*), the lateral cerebellar tract, *KS*, degenerates upwards towards the brain (fig. 123); no such degeneration follows injuries to the spinal cord below this level. Central diseases of the cord, such as vacuole-formation, induce degeneration of the lateral cerebellar tract by the time they have destroyed Clarke's columns. *Pick* has observed that the cells of Clarke's column (fig. 116, *h*) give off processes which, as nerve-fibres, traverse the lateral column horizontally (horizontal cerebellar bundle, 20), and end in the lateral cerebellar tract. Hence it follows that the lateral cerebellar tract receives most of its fibres from the cells of Clarke's column and from Stilling's nuclei. *Bechterew* is of opinion that fibres pass from Clarke's columns to the posterior columns, and to the cells of the contra-lateral anterior horn.

But we also invariably find fibres scattered in the lateral cerebellar tract which are not involved in ascending degeneration. The meaning of these is not yet clear, but they are most probably descending fibres from the cerebellum (*Marchi*). *Lenhossék* regards them as descending branches of fibres which debouch above the seat of the injury.

Gowers' bundle (first described by *W. R. Gowers*, ascending antero-lateral tract, comma-shaped antero-lateral tract, lateral system of the lateral column of *Bechterew*) begins as low down as the lumbar cord, and shows a continuous increase of fibres from thence upwards. It likewise degenerates in an ascending direction, in many cases at any rate. The fibres which compose it (19) probably originate in the cells of the anterior horn (*f*), and it may well be looked upon as a direct sensory route from the spinal cord to the cerebellum.

The remaining portions of the anterior and lateral columns are made up of short tracts about which very little can as yet be asserted. The **anterior ground bundle** and the **anterior mixed lateral column-zone** (mixed lateral zone) seem to have a similar physiological importance. From the border of the grey substance numerous fibres everywhere bend into these columns, which appear to be made up chiefly of the axis-cylinder processes of column-cells (*l*) (21, 22). It is quite possible that fibres from the anterior horn pass *via* the white commissure to the anterior ground-bundle (*VG*) of the opposite side (23).



In the midst of the lateral column, in front of the lateral pyramidal tract, and on the inner side of Gowers' bundle, is another region in which numerous scattered fibres degenerate after injuries to the cord and not after injuries to the brain. *Loewenthal*, who was the first to describe it, gave it the name of fasciculus intermedio-lateralis, *iS*. Its origin and meaning have not yet been ascertained. Possibly a part of the descending cerebellar tract of *Biedl*, already referred to, should be sought here.

Those fibres of the posterior columns which run parallel to the plane of the cross-section should, with but few exceptions, be regarded as sensory collaterals of the posterior roots. The longitudinal fibres of this region consist for the most part of ascending stem-fibres of the posterior roots on the same side, with, perhaps, a few from the other side, though the proportion of the latter is certainly small. There are, however, other longitudinal fibres, occurring in certain well-defined areas, to be considered in this connection.

Especially, the intra-medullary course of the posterior roots demands closer consideration. Every root, at its entrance, occupies a considerable part of the cross-section of the posterior column on the mesial side of the posterior horn, extending ventralwards nearly to the posterior commissure (root-zone as understood by *Mayer*). As, however, each succeeding root occupies the same space as its predecessors, the fibres of the former are thrust towards the middle, and form at first a ribbon-like strip with its ventral edge touching the inner border of the posterior horn. Each successive root-region becomes poorer in fibres as it ascends, and we may reasonably explain the loss by supposing that the fibres enter the posterior horn. Apparently, also, the contiguous root-regions belonging to different levels in the cord, though distinct at first, become more or less intimately combined on their way to the brain (*Mayer*). Accordingly, we should regard Goll's column in the cervical cord, and the part representing the plexus ischiadicus more especially, as the continuation of posterior roots belonging to the lumbar and lower dorsal cord, and seek in *Burdach's* columns for the posterior root-fibres of the plexus brachialis.

After the posterior nerve-roots have been cut across, degeneration of the fibres of the posterior columns is invariably limited to the same side; whereas both clinical observation and experiment go to prove that the nerves from the skin cross over very soon after joining the cord. It is probable that the posterior columns of the same side are chiefly meant to convey impressions of muscle sense (*J. Wagner*).

Both separately and together the two halves of Goll's column form a wedge with its base outwards. The ventral angle is never a sharp one, for this column tends to spread out and mingle with the ventral region of the posterior column. Its ventral part, however, reaches to the posterior commissure only here and there. The ventral part of *Burdach's* column also stops short of the commissure, and the two together mark off as a distinct area a crescent-shaped tract lying in the concavity of the posterior commissure, the ventral posterior column tract, *vH*, which has little or nothing to do with the posterior roots. It appears to consist of short fibres



(fig. 116, 20), the function of which is to establish a connection between certain cells, *K*, of the grey substance and the segments of the cord above or below them.

Two other constituents of the posterior columns have been mentioned:—

1. The comma-shaped bundle of *Schultze*, a narrow band extending between Burdach's and Goll's columns dorsalwards almost to the periphery, and ventralwards nearly to the posterior horn. It is only present at the cervical end, and quickly disappears in the dorsal part of the cord.

2. A tract which appears near the septum posticum in the lumbar cord (and is especially well seen in the sacral cord) comes into view in the uppermost part of the lumbar cord as a narrow seam alongside of the septum. Farther down it assumes a lenticular shape when cut across,



Fig. 124.—Cross-section through the lower cervical cord, below a transverse lesion. *Marchi's staining*. *B*, Burdach's column; *G*, Goll's column; *PyS*, *PyV*, lateral and anterior pyramidal tracts; *SC*, Schultze's comma.

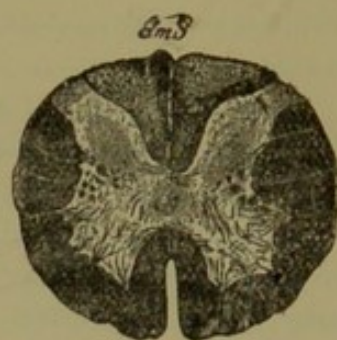


Fig. 125.—Cross-section through the upper sacral cord in sacral tabes. *Pal's staining*. *Dms*, dorso-mesial sacral bundle.

with a flat and a convex side, the flat edges facing each other so as to form an oval in cross-section. In the upper sacral cord it becomes club-shaped, approaches the periphery, and even in some cases projects beyond it. As we proceed down the cord it projects more and more, until at last it can be seen on the surface as a triangular peripheral bundle close to the middle line. The change does not as a rule proceed symmetrically on both sides (see fig. 125). This is the dorso-mesial sacral bundle, *dmS* (oval tract of *Flehsig*, or mesial tract of the posterior column). Some of its fibres can apparently be followed upwards almost to the cervical cord.

The precise meaning of these two tracts is not yet clear. They degenerate downwards, and hence some have sought to find in them the descending branches of the posterior roots. The presence of descending posterior root-fibres has been satisfactorily demonstrated in the case of Schultze's comma, at least; well-marked degeneration having been met with there in cases of extra-medullary disease of the posterior root-fibres.

Another view is that the fibres from the cells of the posterior horn pass along the comma-shaped tract of Schultze. It has also been suggested that the dorso-mesial sacral bundle constitutes to some extent the continuation of the comma-shaped tract.



When the cord is cut across, **secondary degeneration** may be observed in certain regions, differing according to whether the section is taken from above or from below the seat of the injury. We are thus able, by studying degenerations, to distinguish many tracts which under ordinary circumstances are indistinguishable except in the embryo, in which they can be recognised by the different stages at which they acquire the myelin sheath.

(a.) Below a transverse lesion we find **descending degeneration**—

1. Well marked, and to a great depth in the pyramidal tracts (in the lateral pyramidal tract, that is, and the anterior pyramidal tract as far as it goes).

2. Fairly well marked, but only for a short distance in the greater part of the cross-section (short tracts).

3. Usually, if the injury is in the cervical cord, in the comma-shaped tract of Schultze.

4. In the dorso-mesial sacral tract, if it is the lumbar cord which has been injured.

5. In the intermediary lateral-column bundle and (in the upper parts of the cord) in the fibres of the fasciculus sulco-marginalis.

6. Descending degeneration is found in some fibres of the lateral cerebellar tract and in Gowers' bundle.

In secondary descending degeneration consequent upon cerebral lesions, we find hardly any changes except those in the pyramidal tracts, mentioned under 1. As has already been pointed out (p. 236), the area affected in the lateral tract is decidedly smaller than in lesions of the cord.

(b.) **Ascending degeneration** after transverse lesion of the cord is found in—

1. The chief part of the posterior column, that is to say, Burdach's and Goll's columns. The ventral posterior-column tract and the fibres which adjoin it along the mesial border of the posterior horn remain intact, as do also (in most cases) the fibres of the posterior external field and Schultze's comma-tract. Only in lesions of the sacral cord is the dorso-mesial sacral bundle found intact.

2. If the seat of the injury is above the lumbar swelling we find degeneration in most of the fibres of the lateral cerebellar tract and Gowers' bundle.

In lesions of the posterior roots the degeneration affects chiefly those regions of the same side which come under the first head, so far as the injured roots are represented in them. Descending degeneration is also found in the fibres of Schultze's column; the conditions in the dorso-mesial bundle are less clearly understood. Many of its fibres certainly remain intact in disease of the posterior roots. Thus, in lesions of the lumbar and dorsal roots, almost up to the upper dorsal cord, the degeneration affects Goll's column exclusive of the dorso-mesial sacral bundle, and in lesions of the cervical roots it affects Burdach's column. Besides those enumerated, other degenerations in overwhelming number and bewildering variety have been discovered and described as the consequence of severance of the nerve-



roots. Of such are degeneration of remote anterior roots (*Pellizzi*), of the posterior and anterior commissure, and of both lateral cerebellar tracts (*Loewenthal, Pellizzi*); the significance of which is by no means clear.

It remains to recapitulate the fibres which enter into the formation of the **white commissure**; the following bundles may be looked for in it (*cf.* fig. 116):—

1. Anterior root-fibres coming from the fusiform cells (*a*) on the mesial side of the opposite anterior horn, as well as some from other cells of the horn, 1.

2. Fibres passing from the anterior pyramidal tract (*PyV*) of one side to reach the lateral pyramidal tract (*PyS*) of the opposite side, 15.

3. Fibres passing from the commissural cells (*h*) of the grey substance to the antero-lateral column of the opposite side, 14.

4. In animals, at any rate, collaterals of the anterior and lateral columns are supposed to cross in this commissure.

[There are several points of fundamental importance upon which we need information with regard to the columns of white fibres which surround the grey matter of the cord, but of which we are unfortunately unable as yet to give an account. The development of the fibres which compose these columns is still wrapped in mystery. The rudiments of the white sheath of the cord appear very soon after the grey matter is first recognisable as such. The white matter exhibits in its earliest condition a distinct radial striation, an appearance which is exaggerated by the arrangement of the nuclei of its embryonic myelin-cells and neuroglia-cells in radiating rows. Into this tissue penetrate the fibre-processes of the neuroblasts, most of them being undoubtedly on their road to form peripheral nerves. Whether or not any of the neuroblast processes turn upwards or downwards in the cord cannot be stated at present. However probable it may be, therefore, that the longest ascending fibres are processes of cells in the cord, while the longest descending fibres are the processes of cells in the cortex of the brain, short fibres in like manner having their trophic cells on the side from which they carry impulses, no conclusions on these points can be based as yet upon histogenetic data.]

#### 4. VESSELS OF THE SPINAL CORD.

The spinal cord is partly supplied with blood by arteries which come from the vertebral arteries, partly by branches coming from the intercostal, lumbar, and sacral arteries, which enter the spinal canal through the intervertebral foramina and reach the cord along the anterior and posterior roots.

Just before the junction of the two vertebrals, to form the basilar artery, a somewhat slender branch arises from each of them (or not infrequently from one only), inclines across the ventral surface of the medulla oblongata towards the artery of the opposite side, and reaches the anterior fissure usually on the cerebral side of the upper cervical cord. Here the



two vertebro-spinal arteries unite into the unpaired *arteria spinalis anterior*, which can now be followed caudalwards as far as the *conus medullaris*. It corresponds to the anterior fissure. Occasionally this union between the two vertebro-spinal arteries takes place lower down the cord, at the level of the fourth, fifth, or even sixth spinal nerves, or, on the other hand, the vessels separate and reunite repeatedly.

The affluents which discharge into the *arteria spinalis anterior* are carried to the ventral side of the spinal cord along the anterior roots. Their number, although variable, is always small; sometimes there are only three, but they are of considerable size. The most posterior is always the largest. This *arteria spinalis magna* is to be found, according to *Adamkiewicz*, between the eighth dorsal and third lumbar vertebræ on either side.

From the anterior spinal artery, *Spa* (fig. 126), frequent strong branches pass at right angles into the anterior fissure, the *arteriæ sulci* (*s*). Other small branches (*arteriæ radicinæ*) course laterally along the anterior roots to take part in the formation of a plexus on the surface of the lateral column.

The relation of arteries to the dorsal surface of the spinal cord is somewhat different. Here, too, an artery (*arteria vertebro-spinalis posterior*, or *arteria spinalis posterior*) arises from each vertebral artery, but in this case it lies to the outer side of the posterior spinal roots, and does not join with the artery of the opposite side. The arteries are not, however, independent of one another, for they form a chain of anastomosis both on the lateral and on the mesial side of the posterior roots; and these anastomotic chains are not only united together by numerous cross-branches, but they receive minute affluents from without along the course of almost every posterior root. Arterial twigs also pass from these vessels mesially towards the posterior longitudinal fissure, whilst others join the lateral plexus already mentioned.

At the *conus terminalis* a rather large lateral branch comes off from each side of the anterior spinal artery (*rami cruciantes* of *Adamkiewicz*), which anastomoses with the arteries on the dorsal surface. Striking, too, is the zigzag course of the arteries in the region of the *conus medullaris*.

The different branches and twigs which are spread out in the *pia mater* on the surface of the cord are characterised by the numerous anastomoses, some finer, some coarser, which they form.

Amongst the numerous veins on the surface of the cord the unpaired *vena spinalis anterior* deserves especial mention. It runs parallel with the artery of the same name.

Passing on to the **blood-vessels in the interior of the spinal cord** (fig. 126) attention is to be called to the great wealth of vessels in the grey substance as compared with the white.

All the arteries in the cord-substance can be arranged in two systems: (1) those in the zone of the *arteriæ sulci*; (2) those in the zone of the *vaso-corona* (*Adamkiewicz*).

The *arteriæ sulci* advance from their origin in the *arteria spinalis*



anterior (*Spa*) to the bottom of the anterior fissure, where they turn on the ventral side of the white commissure, either to the right or left (bifurcation is rare according to *Kadyi*), as the arteriæ sulco-commissurales, *sc*. These go into the grey substance of the anterior horn, where they break up into a close capillary network, which occupies the greater part of the cross-section of the grey matter. The portion of the white substance which borders on the grey also receives, according to *Kadyi*, branches from these arteries. One branch of especial size (*cl*) goes to Clarke's column, of which it is the exclusive supply. Soon after its entrance into the grey substance each sulco-commissural artery gives off brainwards a considerable anasto-

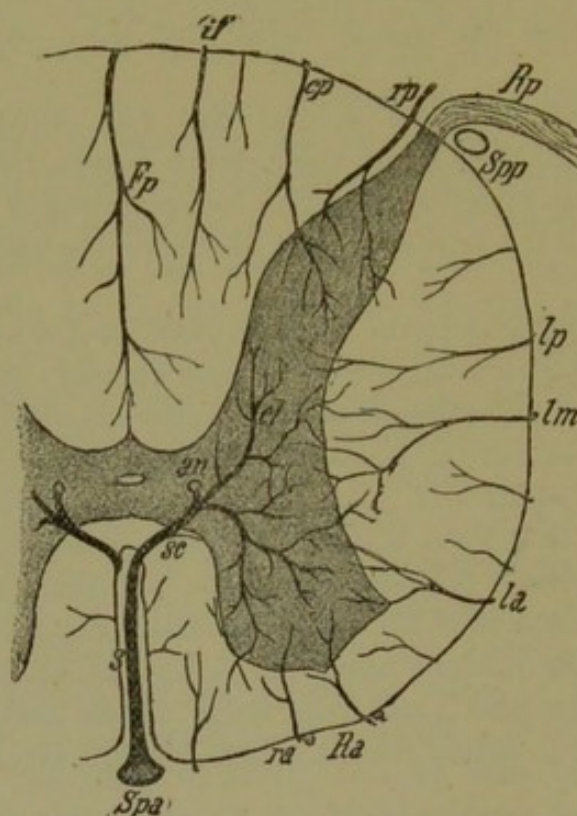


Fig. 126.—Arteries of the spinal cord. *Ra*, anterior root; *Rp*, posterior root; *Spa*, a. spinalis anterior; *Spp*, a. spinalis posterior; *s*, a. sulci; *sc*, a. sulco-commissuralis; *an*, anastomotic branch of the same; *cl*, columna vesicularis; *Fp*, a. septi posterioris; *ra*, a. radicum posteriorum; *cp*, a. cornu posterioris; *if*, a. interfunicularis; *la*, *lm*, *lp*, a. lateralis anterior, media et posterior.

motic branch, and a like branch in the caudal direction; in this way an uninterrupted anastomotic chain is formed through the whole length of the cord. Formerly it was thought that the spaces at the sides of the central canal, which are for the reception of these arteries and their accompanying veins, were only destined for longitudinal veins (the central veins).

Under the title of vaso-corona may be included all the arterial branches which stream in a radiate manner into the substance of the spinal cord from the periphery. Of these, the finer are destined for the white substance only, while the coarser reach to the grey matter. The peripheral portions of the grey matter, like the adjoining parts of the white columns, receive their branches from both systems in an irregular manner. This



debatable ground comprehends about a third part of the cross-section of the cord (*Kadyi*).

The arteria fissuræ posterioris, the largest of the branches belonging to the vaso-corona, runs in the septum posterius nearly up to the grey commissure, supplying numerous branches to both sides.

Usually a large artery, *if* (arteria interfunicularis), courses in the septum paramedianum between Goll's and Burdach's columns; on the whole the more important branches are to be found in the gleial septa. Arteries also accompany the anterior and posterior roots to the grey substance, *ra*, *rp* (arteriæ radicum ant. et post.). The latter, arteria radicum post., also supplies the substantia gelatinosa Rolandi. An artery on the mesial side of the posterior root traverses Burdach's column and loses itself in the caput cornu posterioris, *cp* (arteria cornu posterioris). Two fairly constant arteries extend from the pia mater into the lateral column and the adjoining grey matter, the arteriæ laterales anterior (*la*) et media (*lm*), the latter corresponding to about the middle of the lateral column. An arteria lateralis posterior (*lp*) is less constant. The veins follow, on the whole, the course of the arteries; the venæ sulci, however, are not of sufficient calibre to accommodate all the blood admitted by the arteriæ sulci; the rest goes into the veins of the vaso-corona, and so to the posterior part of the periphery of the cord (*Kadyi*).

## 5. PATHOLOGICAL CHANGES IN THE SPINAL CORD.

The diseases of the spinal cord, which are interesting from the standpoint of pathological anatomy, can only, owing to the abundance of material, receive a cursory notice in this place.

Pathological changes in the cord may either originate within itself or may extend into it from other organs—*e.g.*, brain, nerve-roots, bones, meninges. Hence primary and secondary lesions are distinguished.

There are also some primary diseases of the cord accompanied by co-ordinate changes in other parts of the nervous system. We have instances of this in polyneuritis and disseminated sclerosis. These must, of course, be included among primary forms of disease.

In earlier times, when spinal disease was ill-understood, both from the pathological and the anatomical point of view, most primary diseases of the cord were classed together under the name of myelitis. Later research revealed ever fresh special forms of disease and withdrew them from the category, until the term myelitis was restricted to a very narrow range.

Recently, however, a retrograde movement, if we may so call it, has set in. We learn to recognise more and more special types of disease which, though apparently distinct, must be ultimately referred to a myelitic process, and which generally represent stages transitional to other inflam-



matory changes. The line of demarcation thus becomes fainter and fainter.

Great stress used to be laid upon the distinction between diffuse and systematic disease.

It is characteristic of localised diseases of the spinal cord that they are confined to well-marked regions of the white or grey matter—morphological regions—the limits of which are not at first overstept, and hence reciprocally much information as to the definition of these regions is obtained by a study of their diseases. Diffuse diseases do not respect these boundaries.

It becomes, however, more and more evident that purely systemic disease is largely, if not entirely, secondary in character; and it is difficult to see why a mischievous process in the spinal cord, such as one of the still hypothetical toxine poisonings, should select certain tracts for its point of attack, leaving contiguous tracts unharmed.

Accordingly, we will draw our first distinction between primary (endogenous) and secondary (exogenous) diseases.

## I. PRIMARY DISEASES OF THE SPINAL CORD.

(a) **Inflammatory Processes.**—1. **Acute diffuse myelitis** has either a traumatic origin (as in concussion of the spinal cord); or is toxic, due to the poison of syphilis, tetanus, gonorrhœa, typhus, small-pox, malaria, etc. Owing to its greater richness in blood-vessels the grey matter is usually more affected than in cases of a secondary character, in which the process spreads inwards from the meninges. Complete softening of the cord extending a long way in a longitudinal direction may result from such a myelitis.

In the first stage of acute myelitis the blood-vessels are full and distended, and white corpuscles abound in the lymph-spaces about them. These corpuscles soon disperse throughout the whole inflamed area, though remaining most numerous in the neighbourhood of the vessels. Varicose hypertrophy of the axis-cylinder can be discerned in some of the nerve-fibres. The nerve-cells exhibit degenerative processes of various kinds, differing often in cells close together, granular degeneration and homogeneous swelling being the commonest. With the decay of the elements and the inception of softening, fat-granule cells make their appearance, in consequence of the filling of the abundant lymph-corpuscles with the products of decomposition. If then the vessels, full to their utmost capacity and ill-supported by the softened tissue, tear, they present the spectacle of hæmorrhagic softening.

Sometimes we meet with quite small and circumscribed spots characterised by all the marks of acute myelitic change. Here, by proliferation of gleia, the disease proceeds to secondary degeneration.

**Chronic myelitis**, the rarer form of the disease, runs practically the course just described.



Compression-myelitis (as in caries of the vertebræ) must be ranked with the chronic form; but it will be discussed later, as it is of exogenous origin.

2. A form of acute myelitis confined to the grey anterior horns and the parts immediately surrounding them is met with in the **spinal paralysis of children** and **acute poliomyelitis** of adults (atrophic spinal paralysis, *téphromyélie antérieure*). Here, in all likelihood, we have to do with an infectious process. In the former malady the diseased spots are more circumscribed than in the latter, and are almost always confined to the anterior horn on one side. They both consist primarily of a vascular inflammation of the ventral parts of the cord, limited to a particular level and proceeding rapidly to destruction of the large cells of the anterior horn, some of which are occasionally calcified. At the same time the network of medullated nerve-fibres which permeates the whole substance of the anterior horns disappears from the part affected, so that in sections coloured by Weigert's method it can readily be distinguished from the sound grey-stained parts of the grey substance by the lightness of its colour. Secondarily, degeneration of the anterior roots and the corresponding parts of the motor nerves sets in, proceeding towards the periphery and extending to the muscles; together with a thickening of the gleia-tissue in the anterior horns and multiplication of Deiters' cells (sclerosis). The vessels are also sclerosed. In extreme cases the sclerosis may spread to the surrounding white substance. It is doubtful whether there really is a form of poliomyelitis anterior in which the destruction of the nerve-cells is (as *Charcot* supposed) the primary feature.

Progressive spinal muscle-atrophy shows a similar degeneration of the cells of the anterior horn, but it has not been proved to have root in an inflammatory process in the spinal cord.

3. **Disseminated sclerosis** (insular sclerosis, *scélrose en plaques*), fig. 127.

The degenerated spots are of very variable size (they may even occupy the whole cross-section of the medulla), and are conspicuous in fresh preparations by their reddish-grey or brownish colour. After hardening in chrome-salts they turn bright red. They may occur in any part of the cross-section of the cord, and they spread over from the white substance to the grey, and *vice versa*. Sclerosed spots are found at all levels in the cord, although less often in the lumbar region than in those above. Nearly all sclerotic patches in the cord extend to the periphery; patches completely centralised are rare, especially in the grey substance. It sometimes happens that the patches are symmetrical, or that they start from near the sulcus longitudinalis anterior and spread out into the anterior columns on both sides. As a general rule, the progress of such a sclerosed patch experiences no check, and (as in fig. 127) it encroaches upon a part of the grey substance of both anterior horns without a pause. On the other hand, if the process is not very far advanced, it is possible for some fibre-tracts to run uninjured through the sclerosed spot. An example of this may be seen in single bundles of anterior roots in fig. 127, and in the



nervus accessorius during its course through the sclerosed lateral column of the upper cervical cord.

It is, however, doubtful whether we ought to regard disseminated sclerosis as a form of chronic myelitis which results in the formation of a neoplasm of gleia-tissue, and consequent injury to the nervous elements. Many assume the existence of a primary disease of the nerve-fibres. The curious manner in which the spots spread, as seen both in longitudinal and transverse sections, is, however, opposed to this theory. It has already



Fig. 127.—Disseminated sclerosis in the cervical swelling. *Pal's staining. Magn. 3.*

been mentioned that the axis-cylinder process remains intact to an advanced stage of the disease; secondary degeneration proceeding from a sclerosed spot is consequently not present at first. The nerve-cells, which are also attacked comparatively late, may show every change proper to myelitis (*cf.* the section which treats of pathological change in the nerve-cell); the vessels appear thickened and sclerosed, the spaces they occupy are

usually enlarged. In acute cases, which are not very common, it is easiest to see that, as a matter of fact, these sclerosed spots result from a myelitic process. For the rest, an enlargement of old spots and a constant formation of fresh ones appears frequently to take place even in chronic cases, so that, though the disease may be of long standing, we may come across border zones of fresh degeneration, and even entirely fresh spots, with apparently all the characteristic signs of acute myelitis.

Many attempts have been made to refer disseminated sclerosis back to a primary meningitis; but the grounds for this theory are by no means adequate, since the pia mater may retain a relatively normal character even in the neighbourhood of large sclerosed spots. It is also probable that the pathological process of disseminated sclerosis is not of the same type in every case.

Insular sclerosis generally attacks both brain and cord at the same time, often including the nerve-roots also. The sclerosed patches in the brain are sometimes very large and numerous; they are found chiefly in the region of the pons and in the white substance of the hemisphere. Often the ependyma of the lateral ventricle is the starting-point of large lesions.

**4. Amyotrophic lateral sclerosis** has also been referred to an inflammatory origin. In this case the myelitic process attacks not only the anterior horn, but also the medullary sheath of the cord, especially the lateral and anterior pyramidal tracts. It can, however, be followed into the brain, so that, besides diffuse degeneration of the medullary substance, we meet with strongly-marked descending degeneration of the pyramidal tracts.

**5. Spinal abscess.**—This uncommon disease results either from myelitis of traumatic origin or from a metastatic process. Or it may be



preceded by purulent meningitis, and pass over secondarily to the substance of the cord. The seat of such abscesses is usually central.

(b) **Non-Inflammatory Primary Diseases.**—Of these we will mention :—

1. **Anæmia** and **hyperæmia** of the cord. Extreme anæmia soon leads to the destruction of the nerve-cells and the fibres which arise from them.

2. **Hæmorrhage** into the substance of the spinal cord (apoplexia spinalis, hæmatomyelia) occurs spontaneously (in which case it affects the grey matter and immediately adjoining white substance more especially), as the result of injuries or diminished atmospheric pressure, or it may be secondary to myelitis. It is commonest in the central grey substance and in the posterior horn; in the latter region it is usually confined to one side. In the white substance the most usual seat of hæmorrhage is the ventral part of the posterior columns. If the rest of the cord be healthy the effused blood shows a tendency to spread through the cord in the direction of its long axis, 'tubular hæmorrhage,' a circumstance due rather to the peculiar structure of the grey substance than to the erect posture in Man (*Schlesinger*). Capillary hæmorrhage rarely occurs in the cord. It may be found in the cervical cord of persons who have been hanged.

3. **Paralysis agitans.**—The most characteristic token of this disease is a perivascular sclerosis. Endoarteritis and periarteritis are found in many vessels in the posterior and lateral columns, especially in the ventral part of the posterior column, and again very markedly in numerous vessels in the lumbar cord and in the cervical swelling. From the parts surrounding the vessels a gleial proliferation spreads among the nerve-fibres, presses on them, and so induces sclerosis. In a milder form these symptoms are found in aged persons as the expression of senile involution.

4. Other **diffuse diseases of the blood-vessels** must be mentioned, such as the formation of numerous miliary aneurisms (*Hebold*), a very rare disease, but observed by *Koehler* and *Spitka* throughout the whole length of the cord.

5. **Tumours** of the spinal cord generally commence in the membranes, but we occasionally meet with some which have developed (often as metastases) in the nerve-substance itself. The commonest of these are tubercles and gliomas; sarcoma and syphiloma being rarer. *Kronthal* found a lipoma in the lateral column of a rabbit, and in a case of syringomyelia *Gerlach* observed a small teratoma in the cervical cord. An intramedullary tumour can grow to a comparatively large size at the expense of the nerve substance without noticeably increasing the circumference of the cord.

6. Here, too, **teratological** congenital changes may find a place.

Deficient development of the spinal cord is not rare, especially as regards the grey matter. Asymmetry of the two halves, prolongation of the anterior horns to the periphery, and other defects are found. Many of the most striking distortions, such as occur when one half of the cord appears to be double, are artificially produced by unskilful handling of the cord (*Ira*



v. *Gieson*). Cases in which the two vesicular columns of Clarke are situate in the posterior commissure, nearly touching one another in the middle line, as was first described by *Pick*, have been repeatedly found. *Pick* also described a very rare heterotopia of grey gelatinous substance. In another case, *Musso* found in the posterior column a little heterotopic lesion, which did not quite correspond in structure with the column of Clarke, but was connected with this column of cells by a narrow grey neck.

The student must be on his guard against mistaking for heterotopia of the grey substance the free scattered nerve-cells, which I have already spoken of, as occurring in the medullary substance, and which are far from uncommon.

The condition known as **hydromyelia** (fig. 128) consists in a congenital dilatation of the central canal, the cavity being lined almost throughout with a distinct layer of epithelium.

7. A peculiar kind of cavity formation in the cord, known as **syringo-myelia** (fig. 129), may well be described in connection with hydromyelia. In this one finds in the interior of the cord a tubular cavity, often of considerable size, and extending a long way down the cord. It always lies to the dorsal side of the central canal, although the canal not infrequently opens into it. It has, as a rule, a fairly firm wall, like that of a cyst, and its lateral enlargement usually extends into the posterior horns, though a part of the anterior horn is often included. Such a cavity results from

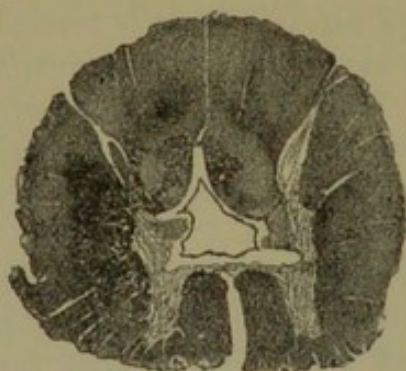


Fig. 128.—Hydromyelia (after *Schlesinger*). *Pal's staining*.

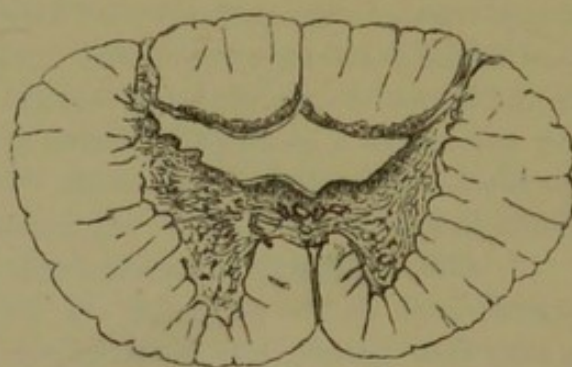


Fig. 129.—Syringo-myelia (after *Schlesinger*). *Carmin-staining*. The central canal lies in the grey commissure in front of the cavity, which extends into both posterior horns.

various causes, or it may be due to deficient development of the cord. We find every intermediate stage between this condition and pure hydromyelia. Syringo-myelia may be caused by a pre-existing primary central tumour (usually a glioma), in many cases, perhaps, congenital, which creates a cavity by destroying the tissue of the cord. At one time the terms syringo-myelia and central gliosis of the cord were used indifferently for everything which led to the same anatomical result. This was an error: there are cases of syringo-myelia without glioma, and of gliomatosis without central softening. Central hæmorrhage and diseases of the intraspinal vessels also seem to have an important bearing upon the formation of such cavities.



8. Senile atrophy is almost impossible to detect microscopically, even in the cord of very old persons, on account of the extremely variable proportions of the normal cord. The signs discoverable under the microscope are a great abundance of amyloid bodies, atrophy and accumulation of pigment in the nerve-cells, and the changes characteristic of old age in the vessels (*vide supra*: Paralysis agitans), which may result in spots of thrombotic softening. But in many very aged persons none of these tokens, except the amyloid bodies, are present, or they are present only to a very limited extent.

9. Many other diseases of the cord, the origin of which has not yet been ascertained, but which are, in all likelihood, primary, might be enumerated here. Such are certain forms of combined systemic disease (see p. 246), the affection of the posterior columns in pernicious anæmia (*Lichtheim, Nonne, Minnich*), ergotism (*Tuczek*), etc.

## 2. SECONDARY DISEASES OF THE SPINAL CORD.

1. *Tabes dorsalis* is not confined to the spinal cord; the peripheral nerves are affected as well, as are also many parts of the brain, especially the cerebral nerves and (in some cases) their nuclei. It is in the cord, nevertheless, that the most serious ravages of the disease are seen.

Roughly speaking, it may be defined as degeneration of the posterior root-fibres in their intra-medullary course. Long ago, Leyden pointed out the connection between the posterior roots and what was then called sclerosis of the posterior column; but to the labours of *Marie, Dejerine*, and *Redlich*, we owe it that we can now assert that tabes affects, in the first instance, only such parts of the cross-section of the cord as can be shown to consist of posterior roots and their collaterals. Accordingly, we find degeneration in the regions into which the roots enter, or through which they pursue their brainward course, in Burdach's and Goll's columns; that is to say, in cases in which the upper extremity is not affected, Burdach's column remains intact. The ventral posterior column tract also escapes, at least in part and in the earlier stages, and so do the two columns which degenerate downwards, and some fibres in the vicinity of the posterior horns.

On the other hand, we observe degeneration in *Lissauer's* border zone, and the reflex collaterals, and shrinkage of the cells of Clarke's column and of the nuclei of the posterior horn.

These changes unmistakably indicate a process of ascending secondary degeneration of the posterior roots. The main difficulty was felt to lie in their pathogenesis.

If we regard as primary the degeneration so often met with in the peripheral nerves, it is hard to understand how it can extend beyond the cells of the spinal ganglia. Moreover, it is seldom as well marked as the degeneration of the cord. This consideration has led some observers to place the seat of the primary disease in the cells of the spinal ganglia (*Marie*).



But anatomical methods of investigation bring to light in the spinal ganglia nothing adequate to explain the extreme intra-medullary degeneration.

We know, however, that under normal conditions the roots are strongly constricted at the point at which they pierce the pia mater (fig. 118), often to such an extent that the myelin sheath completely disappears. It seems, therefore, not improbable that in many cases the posterior roots are pressed or compressed at their most vulnerable point, either by a meningitic process, or by sclerotic atrophy of the pia mater (due, for example, to the sclerosis of the connective tissues which occurs in the most diverse organs after syphilis), or by an overgrowth of gleia in the cortical layer, or finally to a process of sclerosis and consequent thickening of the walls of the vessels which nearly always lie close to the roots at this point.

If secondary degeneration proceeds inwards from the point of entrance of the posterior roots, it is easy to see that in cases of no long standing the extra-medullary part of the root will have suffered less than the intra-medullary part.

2. The characteristic feature of **combined systemic disease** is that it attacks several systems at once; though we are bound to admit that a system is a thing as yet imperfectly defined. It is generally considered an essential attribute of combined systemic disease, that it should attack both tracts that degenerate upwards and those that degenerate downwards.

A common form is distinguished by the fact that, like tabes, it affects the posterior columns, and, in addition, the lateral pyramidal tract, the lateral cerebellar tract, and, possibly, Gowers' bundle, in the lateral column. It is a noteworthy circumstance that the degeneration of the pyramidal tracts decreases as they approach the brain, while in the posterior columns the case is reversed. Here we probably have to do with an inflammatory process starting from the meninges, which, without being locally very severe, injures a certain number of fibres. This would explain the increase of degeneration in the lateral pyramidal tract as it descends; a number of pyramidal fibres in each segment being destroyed in this fashion, so that each succeeding segment adds to the total of those destroyed.

In many cases of tabes dorsalis, the lateral column suffers from the pathological process in the pia mater, and a form of combined systemic disease ensues. Degeneration of the posterior and lateral columns is also met with in creeping paralysis.

A similar form of combined systemic disease (usually met with in hereditary ataxy) is that in which Goll's column degenerates *in toto*, in company with the lateral cerebellar tract, Clarke's columns, and a part of Burdach's column. In other combined forms the lateral cerebellar tracts remain intact, and we must therefore refer such cases to a different exciting cause. Whether or not this cause is a primary disease of the column must be left an open question, as many observers do not admit the existence of such a disease. Those who hold to the notion of primary systemic disease, would describe forms unquestionably secondary, as combined pseudo-systemic degeneration. *Marie* is of opinion that disease of certain areas in the cross-



section, such as is found in pellagra (*Tuczek*), should be attributed to the destruction of the corresponding columnar cells, and consequently to a lesion of the grey substance.

3. Other secondary inflammatory diseases of the cord have been mentioned in the preceding pages. They depend, as a rule, upon pressure from outside (compression-myelitis), due to such causes as inflammatory thickening of the dura mater spinalis in the cervical region (pachymeningitis cervicalis hypertrophica); or the pressure may be due to the growth of tumours within the vertebral canal, either proceeding directly from the membranes as gummata, myxomata, and sarcomata, or solitary tubercles, lipomatous overgrowth of the peridural fat, or echinococci (generally outside the dura); but by far the commonest causes of these secondary diseases in the spinal cord are troubles affecting the vertebræ,—caries, for instance, or more rarely tumours. The peripheral parts of the cord, which are most exposed to the direct effects of the pressure or the inflammation set up by it, suffer most severely from compression-myelitis, especially in the earlier stages. The interstitial glia-tissue thickens to a coarse mesh, traversed by more or less numerous sound fibres. Gradually, as fat-granule cells appear, more and more nerve-fibres become involved in the general decay, many perishing by hypertrophy of the axis-cylinder.

Meningitis spinalis may, owing to the accumulation of exuded lymph, produce general compression of the cord; or a much more interesting direct concentric extension of the inflammatory process to the spinal cord, myelitis annularis. Various diseases of associated tracts of the cord may, as already mentioned, be attributed to primary meningitis.

4. **Secondary degeneration** has already been discussed. It may take as its starting-point parts remote from the cord—the cauda equina, for instance, or certain parts of the brain.

5. The micromyelia of microcephali finds a place here; the diminution chiefly affects the pyramids and Goll's columns, and depends upon the want of development of the brain (*Steinlechner*).



Fig. 130. — Combined systemic disease of the spinal cord. Section from lumbar region. *Magn.* 3. *Pal's staining.* Both posterior columns, with the exception of the part bordering on the grey matter, as well as the lateral pyramidal tract, and to a very slight extent the whole periphery of the cord, appear diseased.

It is impossible in this place to examine in detail the minute histological changes associated with the diseases mentioned above. The most important facts known with regard to these changes have already been introduced into the chapter on the constituents of the central nervous system. I will only observe that it may be of importance to determine, in any particular case, whether the nervous elements of the spinal cord are the starting-points of the disease (parenchymatous processes), or whether,



on the other hand, the disease commences in the connective tissue or blood-vessels (interstitial processes). This is in many cases a matter of great difficulty.

The occurrence in the spinal cord of fat-granule cells gives rise to appearances which vary with the disease. They are never wanting in dementia paralytica (*Westphal*); but they often occur in other diseases of the brain. They have even been frequently found in diseases of other organs, though in such cases they are said to be confined to the segments which supply the diseased part with nerves. Hardly ever are fat-granule cells scattered equally throughout the whole cross-section. In secondary degenerations they are almost always limited to the diseased columns of fibres.

*Marchi's* method should invariably be included among those employed in investigating degenerations; in many cases it shows the nature of the disease as no other method does; and it is the only one by which incipient degeneration can be detected. As it is extremely sensitive, I would again remind the student that its results must be received with caution.

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Owing to the extraordinary richness of the literature relating to pathological anatomy, we can only mention here such works as are referred to in the text.



## SECTION V.—TOPOGRAPHICAL EXAMINATION OF THE BRAIN.

It is not, as a rule, necessary to obtain an unbroken succession when making a series of sections; at any rate when working with human brains or the brains of the larger mammals. Such an attempt would result in a great waste of apparatus, reagents, and time. It is sufficient to take somewhat thick pieces at different levels, from each of which the finest sections possible are prepared. Care must be taken, however, not to discard material in such places as show important anatomical changes within a small area; as, for instance, in the region of the decussation of the trochlear nerves.

When, however, it is a question of establishing minute anatomical relations, as in tracing the course of fibres, we must be careful to prepare an unbroken series of sections. In such cases, as also for pathological work, other methods than those recommended on p. 14 are often valuable.

We shall begin by examining a section obtained from the brain-stem in front of the anterior corpora quadrigemina. The drawings from fig. 132 to 150 are made from carmine-preparations, those from 151 to 153 from sections prepared by Pal's method. The sections are cut in a plane at right angles to the long axis of the medulla. By artificial stretching of a freshly removed brain-stem during the hardening process it is possible to bring the spinal cord and medulla (which naturally make a right angle with one another) into the same straight line. According to *Forel's* method the axis is called 'Meynert's axis of section,' and the perpendicular planes, to which our sections correspond, 'Meynert's cross-planes.' In lower animals this bending of the stem is less, and so the long axis of the spinal cord is more nearly a continuation of the brain-axis.

The comprehension of the complicated structure which the central nervous system presents above the medulla is facilitated by bearing in mind the arrangement, both as to form and course of fibres, which we have found in the spinal cord. Although there are many details in the arrangement of the fibres peculiar to each region, there are yet some general points of view, of which mention may first be made:—

(1.) The tracts of long fibres of the spinal cord can be followed for a longer or shorter distance into the medulla, whence some go to the



cerebellum, and others to the great brain; they are, however, to a greater or less extent, enveloped in other structures.

(2.) The same can be said for the grey matter of the cord, which, with many changes in form, but with no break in its continuity, takes part in the formation of the medulla oblongata.

(3.) Several new grey masses appear with the fibres which belong to them, and introduce varying complications into the picture.

(4.) A striking change is produced in the relation of the several constituents of the medulla by the opening out of the central canal into the fourth ventricle. Structures which were before dorsal to the canal, come to lie on each side of it.

We shall follow the structure of the medulla through a series of sections. But in order not to lose sight of the level at which successive sections are made, it is desirable first to give an account of its external form.

For this purpose it is well to have always at hand a well-hardened brain, and to follow in imagination the planes of the sections as we study them (as shown in fig. 131). It is also desirable to make at the same time cross-sections of a fresh brain, and to study in them the details which microscopic examinations of the prepared brain bring to light.

Changes in formation preparatory to its conversion into the medulla are already visible in the cervical cord at the level of the second cervical nerve. This is about the level at which we usually separate the cord in taking the brain out of the skull-case.

The changes are, as shown in section *a*, fig. 131, still more marked at the level of the first cervical nerves. The posterior horn assumes an almost cylindrical form, while the cervix cornu posterioris, *Ccp*, becomes thinner and the apex disappears. The caput with its substantia gelatinosa Rolandi, *Sgl*, is now separated from the surface by the longitudinally-running fibres of the ascending root of the trigeminus, *Va*; it usually, however, makes a noticeable external prominence, the tuberculum Rolandi (not to be seen in fig. 132).

A strong development of the processus reticularis makes its appearance lower down in the lateral column, as does also the root of the nervus accessorius, XI., which passes from this region to the periphery. Individual bundles of fibres appear cut across at different angles. More and more obliquely-cut bundles are seen, especially traversing the central part of the anterior horn. Still farther brainwards one can see distinctly that large fasciculi from the lateral column pierce the anterior horn, cross the middle line, and add themselves to the anterior columns of the opposite side. These indicate the crossing of the pyramids (decussatio pyramidum), *DPy*. Farther up, the quantity of fibres crossing from the lateral column of one side into the anterior column of the other becomes so immense that the tip of the anterior horn (*Ca*<sup>1</sup>) is completely cut off from its central parts (*Ca*<sup>2</sup>). At the same time the anterior longitudinal fissure (*fsla*) becomes much shallower. In some places it is almost completely filled up. Only that part of the lateral column which we have named the lateral pyramidal



tract shares in this crossing. The bundles which cross ascend obliquely upwards, forwards, and outwards, forming a sharp angle with the mesial, frontal, and horizontal planes alike. Thus it comes about that the anterior fissure is pushed sometimes to one side, sometimes to the other, or it may be so doubled that the crossing of the pyramids is bounded below by a

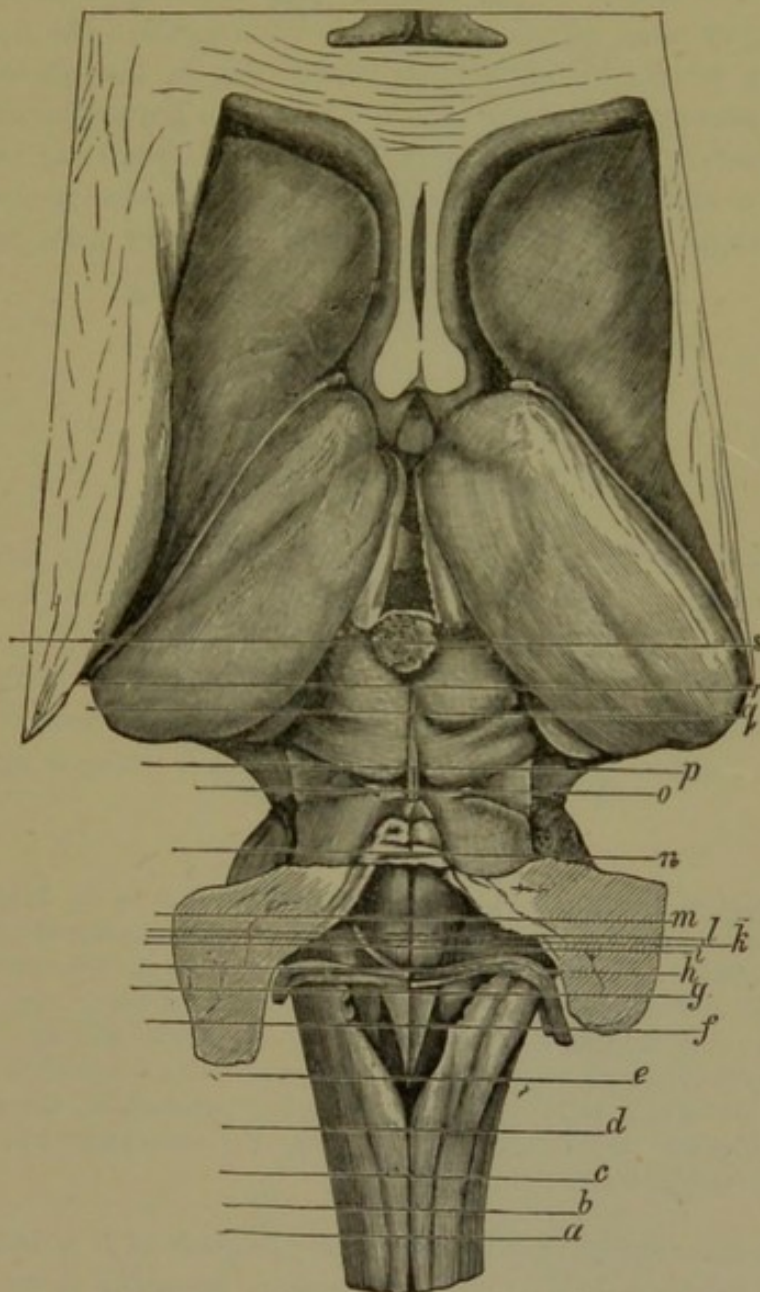


Fig. 131.—Serves to show the level at which the cross-sections, represented in figs. 132-149 (with the exception of 144) are made. It must be remarked that the lines drawn across this figure do not indicate the plane of the cross-sections to which they correspond, but only the situation of their most dorsal portions; cf. fig. 12.

sickle-shaped cleft on either side, and presents a mammilliform process, processus mammillaris (as in fig. 134). The anterior commissure appears to be involved in the overwhelming mass of the crossing pyramids; as a matter of fact, however, it remains independent of the latter, and fibres homologous with it can be followed even as far as the mid-brain.



A transverse section through the region in which the greatest number of fibres cross shows the following changes. With the gradual increase in the cross-section, *Cc*, the central canal (fig. 133), is displaced dorsally. The dorsal border of the central grey substance exhibits two small swellings corresponding to the two portions into which the posterior column is divided. In the mesial of the two columns there appears an elongated club-shaped grey mass, the point of which rests against the mesial of the two swellings which we have mentioned; this is the nucleus funiculi gracilis, *Ng* (post-pyramidal nucleus of *Clarke*, the postero-mesial accessory horn of *Reichert*). A little farther brainwards the lateral swelling increases to a similar nucleus in the cuneate fasciculus (nucleus funiculi cuneati, restiform nucleus of *Clarke*, postero-lateral accessory horn of *Reichert*),

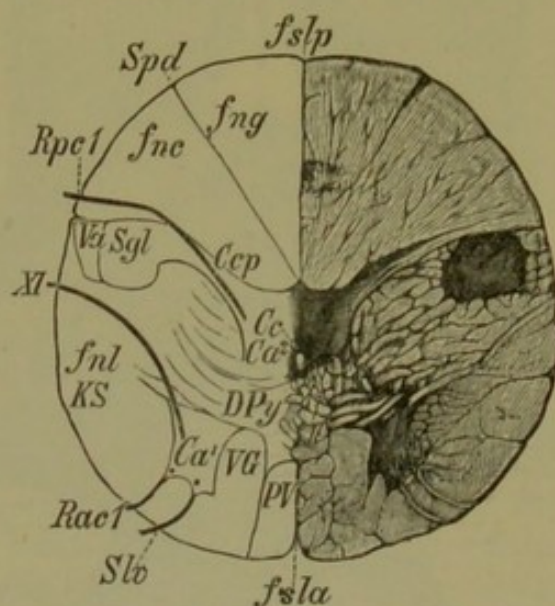


Fig. 132.—Section of the medulla oblongata represented as *a* in fig. 131. *Magn.* 4.—*fslp*, Fissura longitudinalis posterior; *Spd*, sulcus paramedianus posterior; *fng*, funiculus gracilis; *fnc*, funiculus cuneatus; *Rpe1*, radix posterior cervicalis prima; *Va*, spinal root of trigeminus; *Sgl*, substantia gelatinosa; *Ccp*, cervix cornu posterioris; *fnl*, funiculus lateralis; *KS*, lateral cerebellar tract; *Rac1*, radix anterior cervicalis prima; *Slv*, sulcus lateralis ventralis; *fsla*, fissura longitudinalis anterior; *Cc*, canalis centralis; *DPy*, decussatio pyramidum; *Ca*<sup>1</sup> and *Ca*<sup>2</sup>, peripheral and central parts of the cornu anterior; *VG*, anterior ground-bundle; *PV*, anterior pyramidal tract.

resting upon the central grey substance in the form of a wide-based dome. Neither the nucleus gracilis nor the nucleus cuneatus forms a sharply-defined grey mass; both are made up of separate little groups of nerve-cells; an inconstant isolated group of cells, situate peripherally, is known as the outer nucleus of the cuneate fasciculus, *Nce* (fig. 135). Some authorities, however (*Blumenau*, for instance), understand by this term the lateral portion of the nucleus cuneatus, which is occupied by larger cells, preponderating more and more as it approaches the brain.

The lateral column becomes progressively smaller as its fibres cross the middle line to take up their position on the ventral side of the medulla; the lateral cerebellar tracts are seen in figs. 132, 133, 134, lying almost unchanged in the lateral region, while the remainder of the lateral column



is lost in a mass (staining light-red with carmine) which passes over into that portion of the anterior horn which has already been cut off and displaced laterally by the crossing of the pyramids.

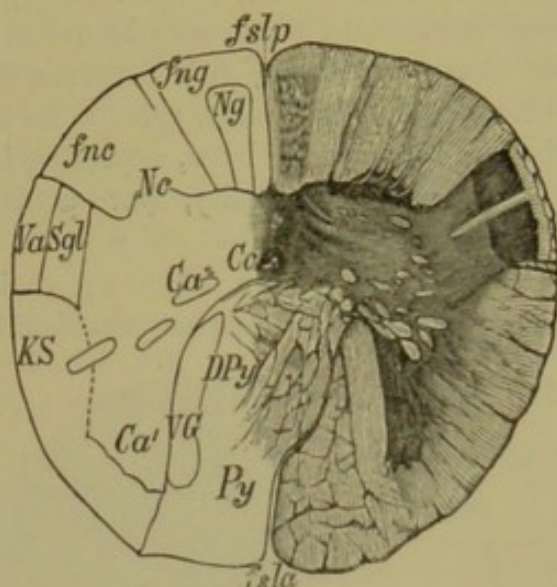


Fig. 133.—Section indicated in fig. 131 by the line *b*.—*Ng*, Nucleus funiculi gracilis; *Nc*, nucleus funiculi cuneati. Other lettering as in fig. 132.

The farther we advance brainwards with our sections, the more indistinct becomes the lateral boundary of this portion of the anterior horn, until at last it loses itself in a mixed region (substantia or formatio

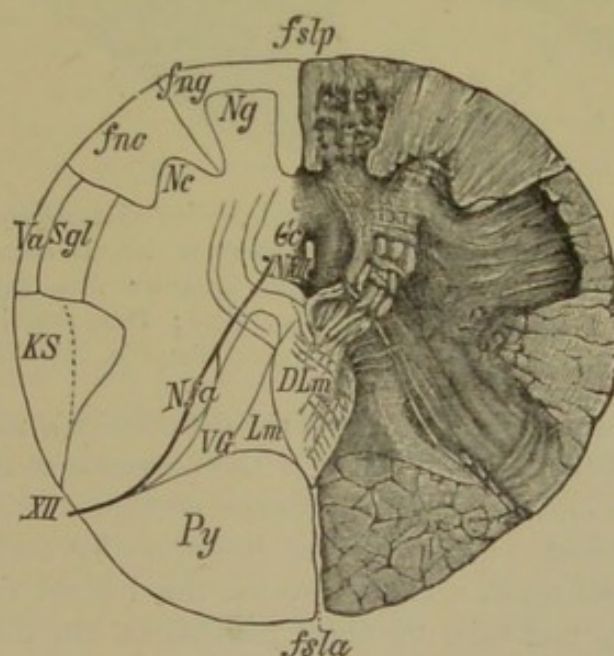


Fig. 134.—Section *c* in fig. 131.—*XII*, Nervus hypoglossus; *NXII*, nucleus of *ditto*; *DLm*, decussatio lemnisci; *Lm*, lemniscus; *Nfa*, nucleus of anterior column; *Py*, pyramids. For remaining lettering, see *supra*.

reticularis grisea, seu lateralis) lying to the side of the ventral half of the medulla.

Mesially this region is bounded by a very distinct white bundle, the



lowest root of the hypoglossal (fig. 134, *XII*), which, starting in the neighbourhood of the central canal, runs ventrally with an inclination sideways towards the periphery. Lying on its inner side somewhere about the middle is to be seen a long, often interrupted, but very conspicuous group of large nerve-cells, which may be called the nucleus of the ground-bundle of the anterior column, *Nfa* (nucleus funiculi anterioris). The ground-bundle of the anterior column retains its original position on the mesial side of the former anterior horn, appearing in cross-section as a fairly recognisable area rounded dorsally, but pointed on its ventral side (figs. 132, 133, 134).

As soon as the pyramids (*Py*) have taken up their position on the ventral side of the medulla, as great compact bundles, the crossing of the

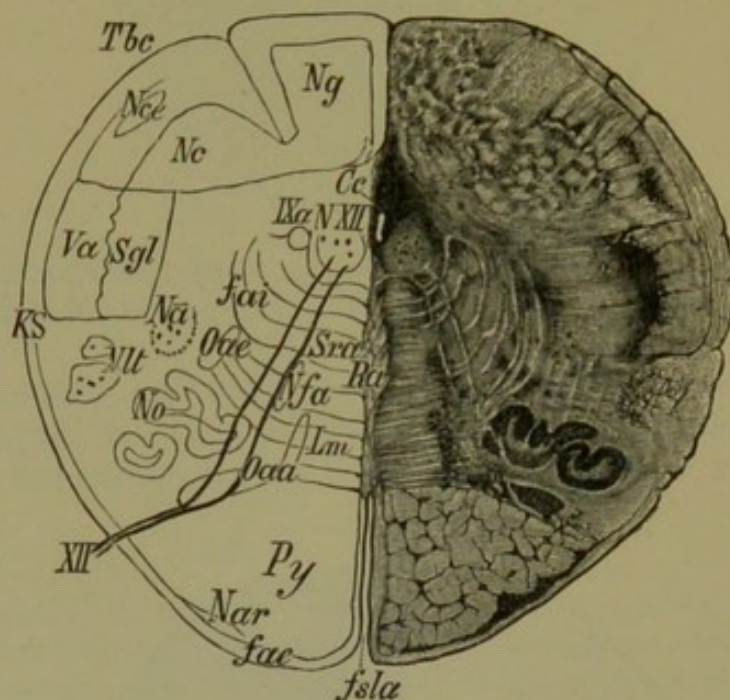


Fig. 135.—Section *d* in fig. 131.—*IXa*, Spinal root of glossopharyngeal; *Nce*, outer nucleus of cuneate fasciculus; *Nlt*, nucleus of lateral column; *Na*, nucleus ambiguus; *No*, olive; *fai*, fibræ arcuatæ internæ; *Sra*, substantia reticularis alba; *Ra*, raphe; *Oae*, external accessory olive; *Oaa*, anterior accessory olive; *fae*, fibræ arcuatæ externæ; *Nar*, nucleus arcuatus; *Tbc*, tuberculum cuneatum.

fillet, *DLm* (decussatio lemnisci, piniform decussation), makes its appearance in the middle line from the back of the pyramids to the central canal. Fairly thick white bundles extend in concentric curves out of the region of the posterior columns, where they are raised up by their two nuclei and surround the central canal. They cross on the ventral side of the canal at an acute angle, and take up their position on the dorsal side of the pyramids in the lemniscus layer (*Lm*).

The crossing of the fillet occurs immediately to the dorsal side of the crossing of the pyramids, so that in adult brains it is impossible to see a boundary between the two; whereas in the embryo the fillet-bundle is recognisable by its early myelination. The crossing of the fillet might be termed the sensory or upper pyramid-crossing.

The tract occupied by the crossing of the pyramids and fillet increases



steadily in its dorso-ventral extension as the brain is approached, becoming at the same time narrower. For a long distance its median diameter is the greatest, and it hence appears as a fusiform area in section. All the way up to the third ventricle the median plane of the brain-stem is occupied by fibres which cross one another at an acute angle, but the area in which this decussation occurs is reduced to a vertical plate, termed the raphe, *Ra*, the dorsal edge of which abuts upon the central canal. The fibres which cross at the most acute angle must, therefore, run almost straight forwards; they are known as the fibræ rectæ of the raphe. Separate fasciculi often diverge from the raphe and run in the same direction some way into the substantia reticularis alba.

In the following sections the smaller groups of grey substance which constitute the nuclei funiculi gracilis et cuneati widen out, so that they make on the surface noticeable swellings; in the fasciculus gracilis the swelling is the cause of the formation of the clava; in the fasciculus cuneatus, the tuberculum cuneatum is the external expression of the grey nucleus. The concentric fibres which before took part in the crossing of the fillets, now constitute thin bundles, all, or almost all, of which come from the posterior columns. Hence the radius of curvature of the outer arcuate fibres becomes constantly greater, and the portion of the medulla lying on the ventral side of the central canal is traversed by these bundles in a characteristic manner.

As these arching fibres no longer have the same meaning as the crossing of the fillets in a strictly literal sense, we simply call them fibræ arcuatæ internæ (*fai*). They traverse the substantia reticularis grisea, cross the roots of the hypoglossus, *XII*, now become more distinct, and divide this region into a number of little fields.

Only a few nerve-cells are scattered on the mesial side of the hypoglossal roots. This region, which extends dorsally to the level of the central canal, consists almost entirely of medullated fibres, and is termed the substantia or formatio reticularis alba (*Sra*) or mesial field of the formatio reticularis. We may assume that the ventral part of the substantia reticularis alba, which, in its dorso-ventral extension, roughly corresponds to the olivary nuclei (now just coming into view), is derived from the crossing of the fillets. Hence its name of lemniscus, or inter-olivary tract. The dorsal part, however, which lies nearest to the central canal, is chiefly formed from the ground-bundle of the anterior column.

Numerous large cells, analogues of the cells of the anterior horn (or, as some would have it, of those of the lateral horn), are scattered about the substantia reticularis grisea; a formation which we may look upon as derived, to a certain extent, from the anterior horn. In certain places the cells are united into compact clumps of grey substance. The groups of large cells which lie midway between the periphery and the central canal, before it opens out into the fourth ventricle in the lateral portion of the medulla, are described as constituting the nucleus ambiguus, *Na* (motor vago-glossopharyngeal nucleus), figs. 135, 136, 137. By far the largest of these cells, especially those which can be more clearly seen in sections



nearer the brain, occupy an area lying laterally to the roots of the hypoglossus and behind the olives. They are not reproduced in the illustrations, as they never form connected groups; but they are sometimes found quite separate from the nucleus ambiguus, and therefore deserve a distinctive name. Perhaps, with *Roller*, we might call them nucleus lateralis medius.

It is well to distinguish from this nucleus the numerous separated masses of medium-sized cells which lie nearer the periphery on the ventral side of the spinal root of the trigeminus, constituting the 'nuclei of the lateral column.'

Here we must again distinguish a fairly compact group of large cells lying close against the spinal root of the trigeminus on its ventral side. From this group (which *Kölliker* supposes to belong to the nervus accessorius) thick fibres originate, and can be followed, often in a conspicuous bundle, for some distance dorso-mesially. This group may be designated nucleus lateralis dorsalis (posterior).

The dorsal boundary of the pyramid is now formed, in its middle portion at any rate, by a long transversely-disposed grey mass which is soon joined at an angle of  $100^{\circ}$  to  $120^{\circ}$  by a shorter sagittally disposed limb, *Oaa* (nucleus of the pyramid, anterior olive), figs. 135 and 136. The sagittal piece (antero-posterior with regard to the sections) has a greater extension brainwards than the horizontal limb (which lies transversely in the sections).

In a section intermediate between those represented in figs. 134 and 135, the nucleus of the pyramid and the nucleus of the lateral column lie very close together. A little farther forward a very characteristic formation of grey matter, the olive, *No* (nucleus olivaris), insinuates itself between them. The olive (figs. 135 to 139) appears in cross-section as a much-folded dentate band curved upon itself with the convexity to the outer side, where it produces on the surface a well-marked swelling ordinarily known as the olive (or olivary body, also inferior olive), *Oi*, figs. 136, 137, 138.

At the periphery of the sections various tracts of fibres are cut in the direction of their length; tracts, therefore, which have a more or less horizontal course. These are the arcuate fibres (fibræ arcuatæ, seu arciformes externæ), *fae*. They have various sources of origin. Many of them curl round the pyramid to join at the bottom of the anterior fissure with the raphe. Often, again, one or other of the fasciculi pierces the pyramidal bundles, and traverses them in an arch of varying width. On the other hand, we meet with bundles, especially at the higher levels, which arise from the raphe and run parallel with the arcuate fibres, but finally enter the pyramids and are absorbed in them.

On the ventral side (and in parts of the lateral side) of the pyramids, certain clumps of grey matter develop in the arciform fibres, about the level at which the convolutions of the olive are first seen in cross-section; the largest of these is in human brains, triangular and very strongly developed, the nucleus arcuatus triangularis, *nar* (anterior nucleus of the pyramid, one of the small pyramidal nuclei of *Stilling*), figs. 135, 136, 137.



The number of these groups of cells, which we shall term nuclei arcuati, increases brainwards, especially on the mesial side of the pyramids, and at last they go over into the nuclei of the raphe or into those great collections of grey matter which we shall come to know later on as the nuclei of the pons. The fibræ arcuatæ externæ receive a considerable addition from the nuclei of the lateral columns, especially from the nucleus lateralis anterior. This streaming of the fibræ arcuatæ towards the nucleus lateralis is helpful in finding the latter group of cells, which is not very well defined.

Superficially-situated tracts of fibres are also found in figs. 135 and 136 in the dorsal portions of the sections. For the most part these belong to the direct (lateral) cerebellar tract which (passing the now quickly-growing

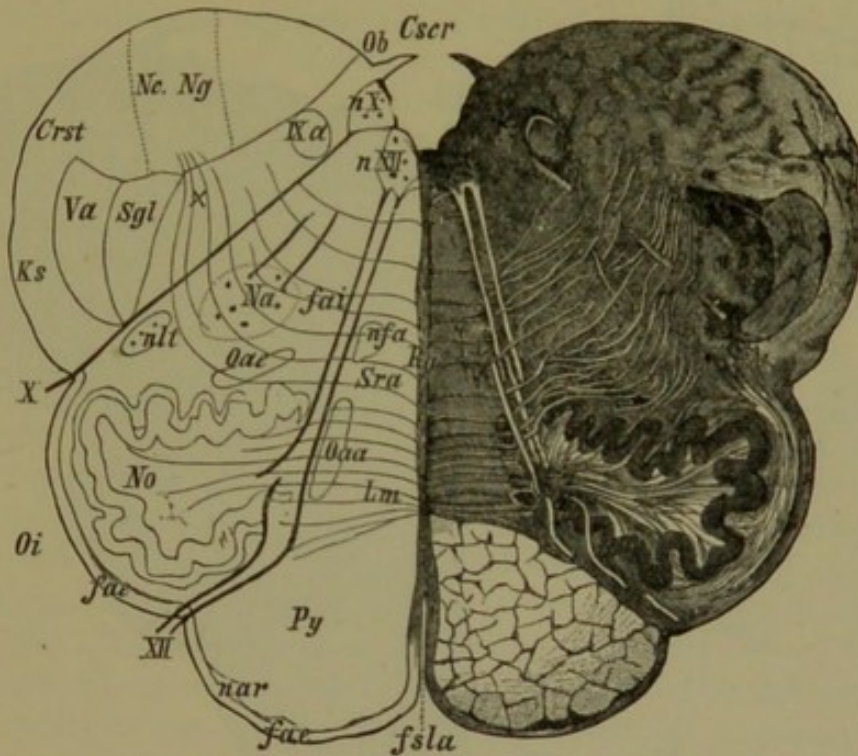


Fig. 136.—Cross-section, fig. 131, *e*.—*Cscr*, Calamus scriptorius; *Ob*, obex; *nX*, sensory nucleus of vagus; *X*, vagus; *Crst*, corpus restiforme; *X*, fibræ arcuatæ from the most external part of the nuclei of the posterior column; *Oi*, olivary eminence.

spinal root of the trigeminus, *Va*), comes into contact with the posterior column, and completely gives up its position in the lateral column.

The substantia gelatinosa Rolandi, *Sgl*, diminishes in amount as rapidly as the spinal root of the trigeminus grows; but it is to be recognised as the companion of the root of the trigeminus, on the concave mesial border of which it lies as far as the point of entrance of this nerve.

A small round bundle, lying on either side of the central canal in the sections through these planes, is still to be described. Farther forwards it becomes a conspicuous isolated tract, round in cross-section, the spinal root of the glossopharyngeal, *IXa* (figs. 135 to 139). From the beginning right up to the cerebral end this bundle is easily recognised by the characteristic loop of nerve fibres (fibræ suprareticulares) which surrounds it on all but the ventral side.

If the section falls not far above the level at which the central canal



opens out into the fourth ventricle (fig. 136) at the calamus scriptorius (*Cscr*), the following points will be noticed:—The grey matter which lies dorsally to the central canal is pushed as the cleft opens to the outer side, being displaced farther and farther outwards as the floor of the fourth ventricle becomes flatter, while the grey matter of the anterior horn, which lay on the ventral side of the canal, travels upwards and comes to occupy the mesial portion of the floor of the fourth ventricle.

The only remains to be found of the embryonal roof of the fourth ventricle are certain little plates of tissue (varying in form and development in different individuals), which are enclosed in pia mater, and rest

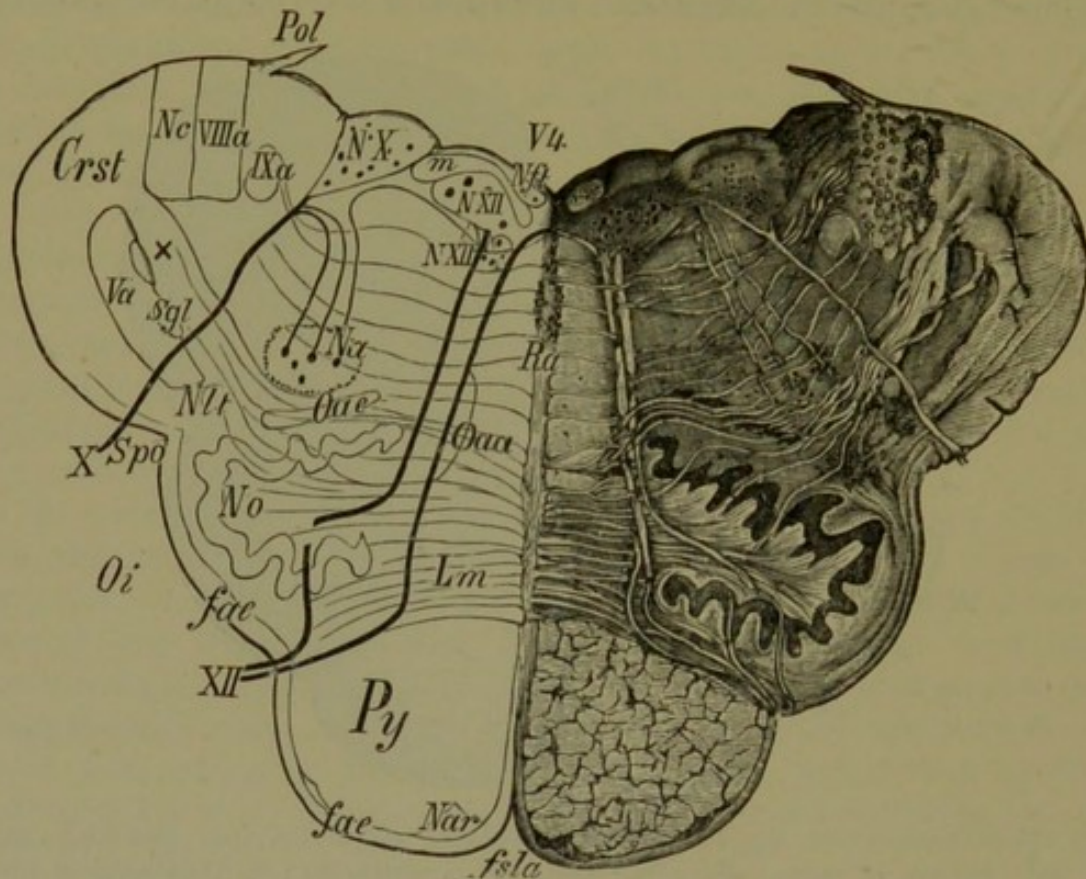


Fig. 137.—Cross-section, fig. 131, *f.*—*Pol*, Ponticulus; *V4*, fourth ventricle; *VIIIa*, spinal root of auditory nerve; *m*, white matter covering the chief nucleus of the hypoglossal nerve (*NXII*); *NXII'*, small-celled nucleus of hypoglossal nerve; *Nlt*, nucleus funiculi teretis; *X*, accession to the restiform body (*Crst*) of fibres from the fibræ arcuatæ internæ; *Spo*, sulcus postolivaris.

against the fasciculus gracilis with their free borders directed towards the inner side (*cf.* p. 68). An inconstant platelet [of white matter] which fills in the angle between the diverging fasciculi graciles is known as the obex, *Ob*, fig. 136. The symmetrical plates in front of this are the ponticuli, *pol* (alæ pontis), fig. 137.

The small collections of grey matter which we have learnt to know as the nuclei of the fasciculus gracilis and fasciculus cuneatus become constantly smaller. Their place is taken by a quickly-growing conspicuous and fissured field of fibres, the corpus restiforme, *Crst*, with which the lateral cerebellar tract blends. The restiform body slopes obliquely upwards and forwards around the outer side of the spinal root of the



trigeminus. Only by embryological investigations can we make out the complicated elements out of which the restiform body is built up; attention must be called, however, to the considerable mass of fibres which passes on the mesial side of the substantia gelatinosa and spinal root of the trigeminus to join the restiform body, the *fibræ arcuatæ internæ laterales*, X (figs. 136 and 137).

By this time the olive has reached its greatest development, and is more conspicuous than anywhere else from the surface. On the dorsal side of the olive proper an extended grey mass has made its appearance in the *formatio reticularis*, the upper or outer accessory-olive, *Oae* (nucleus olivaris accessorius externus *seu* superior), figs. 135 to 138.

The roots of the hypoglossal nerve, *XII*, which spring from large nerve-cells, *NXII* (hypoglossal nucleus or chief nucleus), situate for the most part in the median grey matter in the floor of the fourth ventricle, are now at their greatest development (figs. 136 and 137). They make a sharp boundary between the substantia reticularis alba and substantia reticularis grisea, and course for the most part between the sagittal limb of the pyramidal nucleus (*Oaa*) and the olivary nucleus (*No*). Often they seem to be connected with the latter; in reality they only cross through it or run within it for a certain distance downwards towards the cord, and then bend horizontally and come out in the furrow between the olive and the anterior pyramid. The principal nucleus of the hypoglossal is still separated from the surface of the sinus rhomboidalis by a layer of fine medullated fibres, disposed for the most part in a longitudinal direction. On the mesial edge of the hypoglossal nucleus, and still more on its lateral edge, the cross-section of this white column assumes the shape of a club, *m* (fig. 137). These fibres (the dorsal longitudinal tract of Schütz) give to the hypoglossal triangle on the floor of the fourth ventricle its striking white colour. Close beneath the ependyma and very near the raphe a small group of nerve-cells is cut through, known as the nucleus funiculi teretis, *seu* eminentiæ teretes or nucleus medialis, *Nft* (figs. 134 to 141).

Two groups, not always clearly defined, may be distinguished in the lateral part of the grey floor of the fourth ventricle, *NX* (*Holm*). The dorsal group consists of small cells, the ventro-mesial of large ones. The dark pigmented cells which lie scattered along the periphery also deserve mention. Other tracts of fibres, less considerable than the roots of the hypoglossus, radiate outwards from these groups. Not equally visible in all sections, they pass ventrally to the ascending root of the glossopharyngeal through the substantia reticularis grisea, and usually pierce in a very striking manner the spinal root of the trigeminus *Va* (figs. 137 and 138). These are the root-fibres of the vagus and glossopharyngeal nerves; the grey mass from which they spring is therefore the vago-glossopharyngeal nucleus or dorsal vagus nucleus. A number of fibres originate in the nucleus ambiguus, *Na*, or group of large cells, which lies in the substantia reticularis grisea; first passing dorsally, many of them arch over and join the glossopharyngeal and pneumogastric roots. These groups of cells may



be looked upon as the motor nuclei of *IX* and *X*. Other fibres from these nuclei incline medianwards towards the raphe.

Sections farther forward (figs. 138 and 139) differ in shape from those already described owing partly to the flattening out of the broader floor of the ventricle and partly to the constant increase in size of the corpus restiforme which rises up above its dorso-lateral margin. The last traces of the posterior columns disappear.

At the level at which the root-fibres of the hypoglossal first disappear from the section, the spinal glossopharyngeal root, *IXa* (fig. 138), seems to bend horizontally outwards to make its exit parallel with the other root-fibres of the glossopharyngeal nerve. It is much the strongest bundle of root-fibres belonging to this nerve, and pierces the spinal root of the fifth,

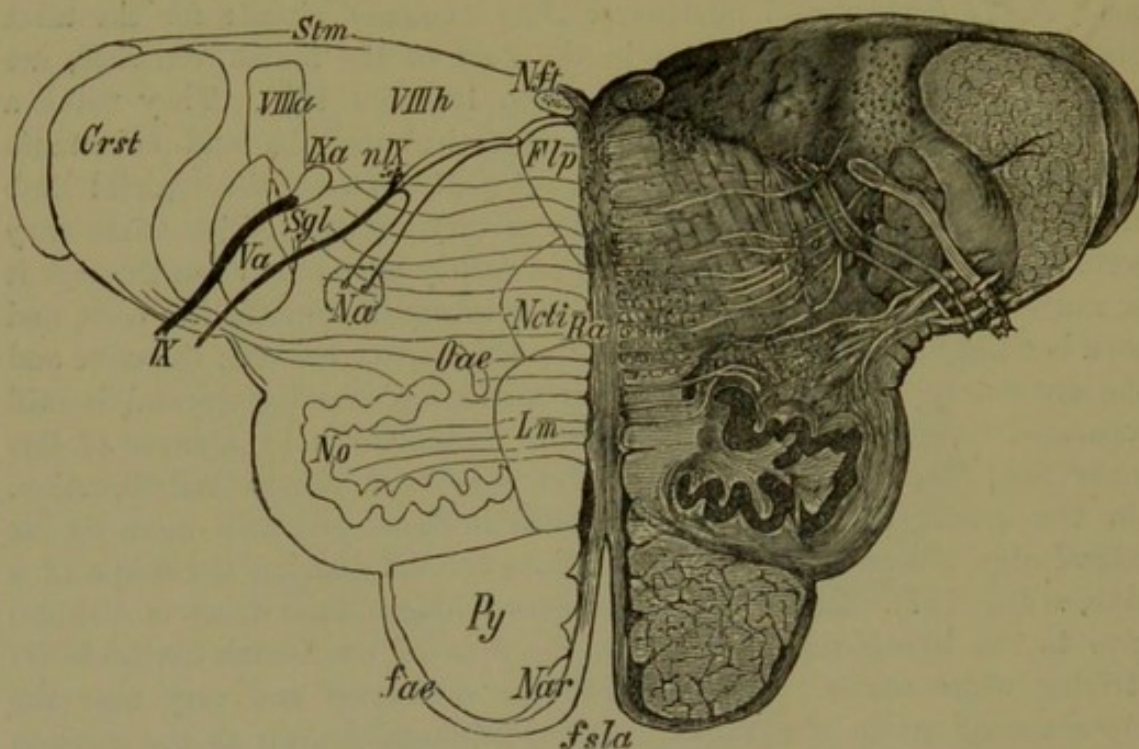


Fig. 138.—Transverse section, fig. 131, *g*.—*Stm*, Striæ medullares seu acusticæ; *VIIIh*, chief auditory nucleus; *IXa*, nervus glossopharyngeus; *nIX*, glossopharyngeal nucleus; *Flp*, fasciculus longitudinalis posterior; *Ncti*, nucleus centralis inferior.

reaching the periphery on the ventral side of the corpus restiform, *Crst*. Gelatinous substance is present in varying amount along the whole course of the spinal glossopharyngeal root, and is collected in a somewhat larger body at the bend. This is the glossopharyngeal centre of Roller. The nucleus ambiguus is still visible as the starting-point of glossopharyngeal fibres; and the cells of the nucleus lateralis are often very conspicuous on the dorsal side of the superior olive.

By this time the hypoglossal nucleus has disappeared from the floor of the fourth ventricle; only the last remnants of the nuclei of vagus and glossopharyngeal are left; but a great triangular grey field occupies the greater part of the region below the fourth ventricle, the apex of which is directed towards the middle line; this is the 'chief' nucleus of the auditory nerve, *VIIIh*. The commencement of this nucleus might have been looked



for in fig. 137, in the region which extends from *NX* laterally as far as *VIIIa*. As it grows in size it presses the nuclei of *IX* and *X* downwards into the substance of the medulla, and at last when the chief nucleus of *XII* gives way to it, it extends itself inwards as far as the middle line. Between the auditory nucleus and the corpus restiforme is seen, in addition to the remains of the funiculus cuneatus (fig. 137), a nearly rectangular area of medullated fibres, transversely cut, embedded in a network of grey matter called the spinal root of the auditory nerve (figs. 137 to 140). Other bundles of fibres of varying thickness, which pass close under the floor of the fourth ventricle over the restiform body, also belong to the auditory nerve, the striæ medullares, *Stm*.

In the course of the striæ medullares are usually embedded larger or smaller masses of grey matter which sometimes make considerable eminences in the neighbourhood of the corpus restiforme (*tæniola cinerea*, *tuberculum acousticum*). When the striæ medullares are well developed it is easy to see that the majority of their fibres, just before reaching the middle line, bend ventrally, descending towards the pyramid in the outer margin of the raphe. In fig. 138 this is only shown to a small extent, at the spot where the letters *Nft* are placed.

No great change in the cross-section of the pyramids or of the substantia reticularis grisea and alba is exhibited by fig. 138. In the substantia reticularis alba, however, we begin to see a distinction between its most dorsally situate longitudinal fibres, *Flp*, which lie close to the floor of the fourth ventricle and the most ventral fibres, *Lm*. This distinction is due to the increasing rarity of the fibres in the intervening region and the accumulation in their place of grey substance, intercalated between the longitudinal and transverse fibres. This grey matter, nucleus centralis of *Roller*, *Ncti* (nucleus centralis inferior), is not sharply marked off from the substantia reticularis grisea.

The smaller division of longitudinal fibres, derived in part from the ground-bundle of the anterior column, retains its position close up against the raphe throughout the whole of the floor of the fourth ventricle and the aqueduct of Sylvius. It is known as the posterior longitudinal bundle, *Flp* (fasciculus longitudinalis posterior). The larger ventral collection of fibres—the continuation upwards of the inter-olivary layer—constantly changes its position in a manner to be presently described.

In sections cut just below the pons, which may be regarded in the ascent of the system as the last sections of the after-brain, the upper convolutions only of the olive, *No*, are to be seen; the transverse diameter of the pyramids, *Py*, is now a little less, but their dorso-ventral diameter is proportionally greater. The triangular nucleus of the auditory nerve, *VIIIh*, retains the same relation as before to the spinal roots of this nerve, *VIIIa*, and of the trigeminus, *Va*, as well as to the restiform body. The restiform body is surrounded more obviously than in fig. 138 by great bundles of fibres which, although they belong to the auditory nerve, are, nevertheless, not to be looked upon as root-fibres; rather they constitute a connection with the great brain of the accessory auditory nucleus soon to



be described. Formerly they were described as constituting the lateral root of the auditory nerve, but, for the most part, this name can only properly be applied to the compact bundle of fibres visible on the ventral side of the accessory nuclei, next to be described. The mesial root courses down

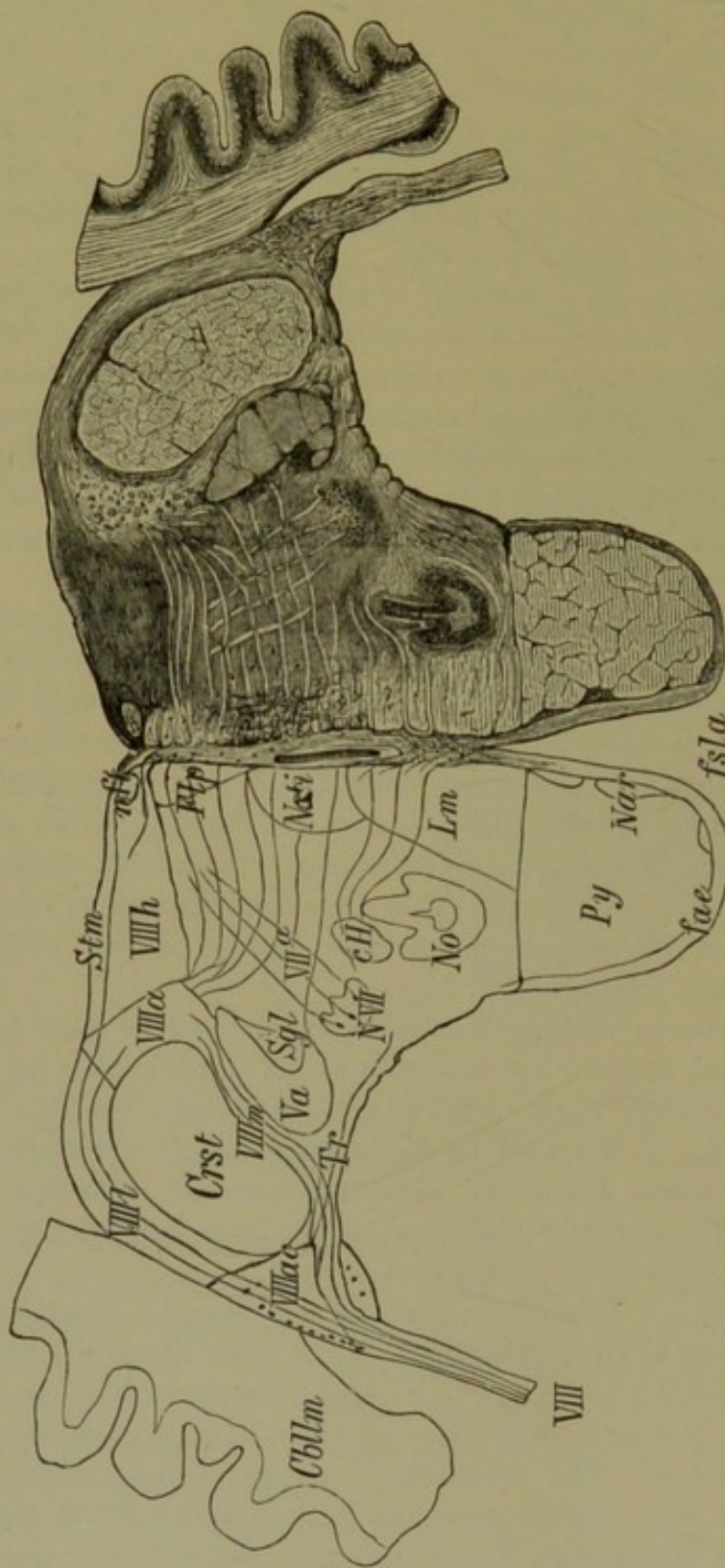


Fig. 139.—Transverse section, fig. 131 h.—*Cblm*, Cerebellum; *VIIIh*, nervus acusticus; *VIIIh*, central tract or lateral root of auditory nerve; *VIIIh*, mesial root of auditory; *VIIIac*, accessory nucleus of auditory; *VIIIh*, chief nucleus of auditory; *Tr*, corpus trapezoides; *NVII*, facial nucleus; *VIIa*, root-fibres of n. facialis (nuclear limb); *cH*, central tract of tegment.

between the restiform body and the spinal trigeminal root. As well in the angle between the mesial and so-called lateral roots as on the inner and outer sides of the conjoined roots appear collections of grey matter, the accessory nucleus of the auditory, *VIIIac*; the auditory roots are especially



characterised by their richness in nerve-cells. Out of the accessory nucleus scattered bundles of fibres course transversely towards the median line ;

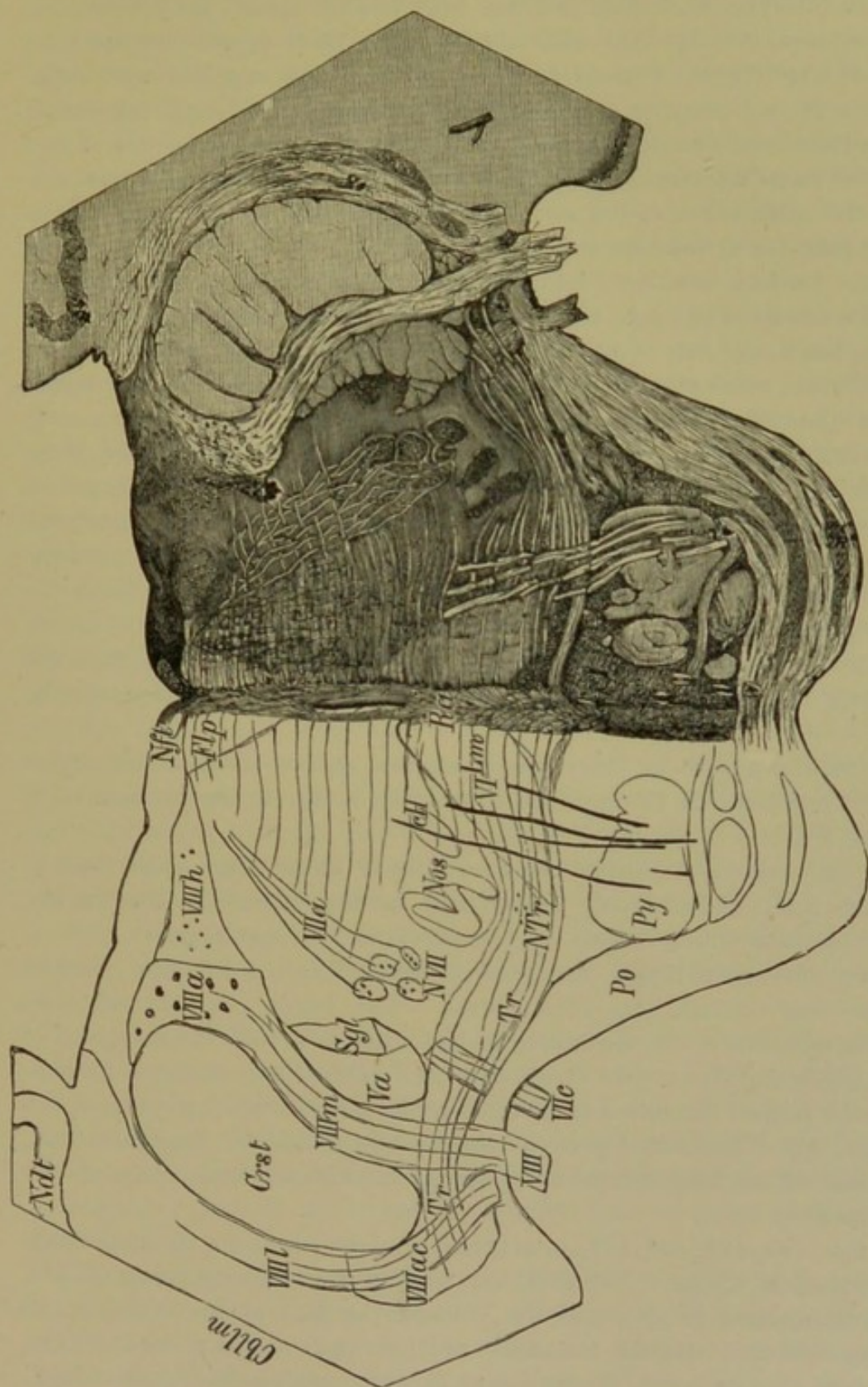


Fig. 140.—Cross-section, fig. 131, i.—*Ndt*, Nucleus dentatus cerebelli ; *VIIIa*, spinal root of auditory nerve and its large-celled nucleus ; *Nos*, nucleus olivaris superior ; *VI*, root-fibres of n. abducens ; *NVII*, nucleus of facial nerve ; *VIIa*, nuclear limb ; *VIIc*, issuing limb of its root ; *NTr*, nucleus corporis trapezoidis ; *Po*, pons.

they belong to the corpus trapezoides, *Tr*, which only attains to its full development in sections higher up the axis.

The separation between the posterior longitudinal bundle and the fillet effected by the nucleus centralis inferior, *Ncti*, becomes increasingly distinct.



After the nucleus of the lateral column has disappeared the groups of cells, which already in posterior sections formed the motor nuclei of the vagus and glossopharyngeal nerves, increase considerably in size, little masses of grey substance, circular and well-defined, make their appearance, and, as soon as the last fibres of these two nerves have been supplied with cells, other fine fibres belonging to another motor nerve, the facial, take their place and are seen coursing dorsally and medianwards. This is the lower end of the facial nucleus, *NVII*, which is nothing more than the continuation of the nucleus ambiguus, and, therefore, indirectly of the cells of the anterior horn [or of the lateral horn].

If our sections are carried through the brain in more anterior planes, they take the form of rings, the ventral half of each of which is formed by the pons, the dorsal half by the cerebellum. Through the ring thus formed, and in organic connection with its lower half, extend most of the structures hitherto described as taking part in the formation of the after-brain. It is manifest that the corpora restiformia, which are columns of fibres destined for the cerebellum, are excluded from this ring. It is distinctive of the pyramids in this region that they intertwine with the fibres of the pons. In examining the human brain it is better to cut off the cerebellum before hardening, leaving only the lingula in connection with the brachia pontis. In monkeys and small animals the cerebellum may be cut in the same sections as the pons (see fig. 16). Hence we exclude the cerebellum at present from this description, and treat it subsequently by itself.

The most conspicuous difference between a section through this region (fig. 140) and sections through the after-brain is due to the appearance of the pons, *Po*.

The pons takes the form of great bundles of white fibres which start in the cerebellum, and running transversely across the middle line enclose amongst them irregular masses of grey substance, the nuclei pontis.

Every section through the pons is divided into two quite distinct portions—one ventral, the other dorsal. The latter contains the continuation upwards of the structures of the hind-brain with the exception of the pyramids and the corpus restiforme; the ventral half contains, in addition to the proper formation of the pons, the continuation upwards of the pyramids, *Py*. The dorsal portion may well be called the tegmental field, since most of its longitudinal fibres appear later in the tegmentum of the crus cerebri.

In figs. 140, 141, and 143, an artificial boundary between the cerebellum and the pons is traced. The chief nucleus of the auditory nerve, *VIIIh*, already diminished in size, still lies beneath the floor of the ventricle; to its outer side the reticular formation of the spinal auditory root, *VIIIa*, has become thicker, and is distinguished in many animals more than in Man, by conspicuous large multipolar cells; this region is, therefore, known as the large-celled nucleus of the auditory nerve (Deiters' nucleus). The mesial auditory root, *VIIIm*, is seen to proceed from the region of the large-celled nucleus and the lateral and ventral angle of the chief nucleus, between the



corpus restiforme, *Crst*, and the spinal root of the trigeminus, *Va*, taking its exit at the lateral part of the pons. The accessory nucleus, *VIIIac*, lies on the convexity of the corpus restiforme, and is traversed a little to the ventral side of this by the lateral root, *VIII*. The transverse fibres which we have already described as connected with this group of cells form the largest part of the corpus trapezoides, *Tr*.

In the lateral part of the reticular substance the facial nucleus, *NVII*, becomes even more distinct. It takes the form of rounded groups of cells, from which separate bundles of fibres, *VIIa*, never united into large tracts, wend their way obliquely in the direction of the dorsal surface and mid-line, towards the posterior longitudinal bundle, as it seems. As they run at the same time somewhat forwards, it is only in later sections that we shall be sure that we have to do with the fibres of origin and the nucleus of the facial nerve. In the same section we see these same fibres traversing the pons obliquely near its margin, *VIIc*, close to the inner side of the spinal root of the fifth nerve, but this time in the form of a compact bundle. The roots of the facial and trigeminal nerves towards their exit are distinguished by their course, the one on the mesial, the other on the lateral side of the spinal root of the fifth.

While in the most distal section through the region of the pons all the fibres of the pons surround the pyramids on their ventral side, we find in sections farther brainwards that scattered bundles of fibres and masses of grey substance, as well as the fillet, insinuate themselves between them. Farther forward still, scattered clumps of grey matter are found embedded amongst the hitherto compact bundles of the pyramid; and, lastly, the farther forwards we make our sections, the more horizontal fibres do we find interlacing with the bundles of the pyramid, as well as lying to their dorsal side. The tracts which lie on the ventral side of the pyramid may be designated superficial bundles of the pons (*stratum superficiale pontis*), those on its dorsal side, deep bundles (*stratum profundum pontis*), and those which traverse it, middle (or piercing) fibres (*stratum complexum*).

In animals the pons is much less strongly developed than in Man. Consequently we find in the former, as a rule, that a considerable portion of the corpus trapezoides is left uncovered, and appears superficially on the ventral side of the medulla as a somewhat trapezoidal area, which occupies the whole space behind the pons and between the ventral margins of the cerebellum; [part of the corpus trapezoides runs over and part under the pyramids].

In the section shown in fig. 140 a number of fairly thick bundles of coarse fibres, *VI*, are to be remarked, which cross the tegment in a dorso-ventral direction, piercing also the fillet, the corpus trapezoides, and the pyramid. Neither their beginning nor their end are shown in this section. These are the fibres of the nervus abducens, the nucleus of origin of which, lying near the great brain, will be seen in fig. 141; while its exit from the medulla just behind the pons would be shown in a section taken between figs. 139 and 140, but not here delineated.







Dorsal to the fibres of the pons lie a number of structures which we have already studied, but may with advantage recapitulate. In addition to the transverse trapezoidal fibres, we find, in order from the middle line outwards:—(1) The raphe, (2) the fillet, (3) the roots of the nervus abducens, (4) the nucleus trapezoides, (5) the superior olive, (6) the nucleus nervi facialis, (7) the issuing fibres of the trigeminal nerve, (8) the spinal root of the trigeminal, (9) the mesial root of the auditory, (10) the restiform body, (11) and (12) the lateral root of the auditory nerve with the accessory nucleus of the same.

On the mesial border of the superior olive is found a small tract of fibres cut transversely, the central tegmental tract, *cH* (*Bechterew* and *Flechsig*). It is not, as a rule, sharply defined. Its fibres are supposed to take origin in the inferior olive.

In the next section (fig. 141) the fillet, which lies just dorsal to the fibres of the pons, is broader, its dorso-ventral diameter being diminished to a corresponding extent. It is traversed in the manner already described by the fine bundles of the corpus trapezoides.

In this section, as in all those behind it, *fibræ arcuatæ* are seen curving through all parts of the tegmental region, from the pons fibres right up to the floor of the fourth ventricle. They traverse the posterior longitudinal bundle, *Flp*, in their course towards the raphe.

One must be careful to avoid confounding with the posterior longitudinal bundle a medullated nerve, *VIIb*, which for a time finds its place between it and the surface of the ventricle. This nerve, the ascending limb of the root of the facial nerve, is easily distinguished from the posterior longitudinal bundle by the fact that it is not traversed by *fibræ arcuatæ*. It is also better defined. Most of the fibres arising from the facial nucleus, which is already much diminished in size, incline at first towards the raphe, applying themselves gradually to the nerve-root as it lies beneath the floor of the ventricle close to the middle line, while at the same time they assume a longitudinal direction.

In this section, too, we see, for a greater distance, the descending limb, *VIIc*, of the root of the facial nerve, laterally to its nucleus. So it comes about that the root of the facial nerve, *VIIa, b, c*, is three times met with on its course from its nucleus to the surface, without the connection between the three pieces being visible in any one section.

Close to the nucleus of the facial nerve in the bay formed by the fibres of the corpus trapezoides lies the superior olive, which here takes the form of a narrow, more or less folded riband.

Near the olive the central tract of the tegmental region is usually but slightly marked, and next to it the bundles of the abducent nerve are conspicuous, as they form arches convex towards the raphe in their passage towards a grey mass, *NVI* (nucleus nervi abducentis), which lies near the middle line, not far below the floor of the ventricle. Owing to their oblique direction spinewards, the fibres of the abducens are only seen in one portion of their course.

It should be mentioned that in this section the mesial auditory root, the



fibres of which take origin in the large-celled nucleus, is still to be seen lying between the spinal root of the trigeminus and the corpus restiforme; the accessory nucleus and the lateral root of the auditory nerve have, however, disappeared. The restiform body, as soon as it is set free from the bands of the lateral root of the auditory nerve, begins to sweep off into the cerebellum. Scattered nerve-cells belonging to the nucleus reticularis tegmenti, *Nrtg*, are found far down in that portion of the substantia reticularis which lies near the raphe, between the fillet and the posterior longitudinal bundle.

In the next section (fig. 142) the nervus acusticus is wanting. Numerous small masses of grey matter, composing the sensory nucleus of the trigeminal (which only reaches its full development in the section following), are seen enclosing the fibres of the transversely-divided nerve. They are of irregular, roundish shape, and are not sharply marked off from the substantia gelatinosa. In order that the relation to one another of the

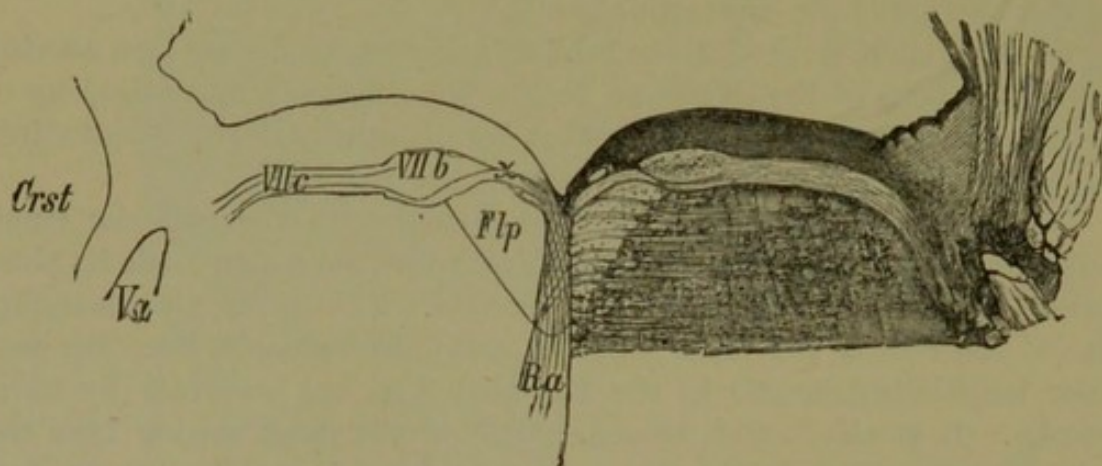


Fig. 142.—Transverse section corresponding to fig. 131 *l*; shows the bending over of the ascending limb of the facial nerve into its issuing limb.

issuing and ascending limbs of the facial nerve may be seen well, only so much of the section as lies near the floor of the fourth ventricle is represented in the woodcut. The way in which the root changes its vertical for the horizontal direction is well seen, as is also the obvious accession at *x* of fibres from the opposite side.

We have now reached the real region of origin of the trigeminus (fig. 143). The section shows us the posterior longitudinal bundle, *Flp*, passing up to the situation which rightfully belongs to it, beneath the floor of the ventricle. The fillet, *lm*, spreads out farther sideways until it nearly touches the cerebral end of the superior olive. Laterally to the olive lies the territory of the trigeminus. The clumps of gelatinous substance already noticed farther spinewards in the substance of the spinal trigeminal root are obviously more numerous and larger. They make up the sensory nucleus of this nerve, *NVs*. Fibres from this spot are seen joining the spinal root; other fibre-bundles coming from the groups of cells also join the great sensory root which traverses the crus pontis (middle cerebellar



peduncle) obliquely ventralwards and outwards, *Vs*. In this section and also in those farther forwards, the sensory root is cut obliquely.

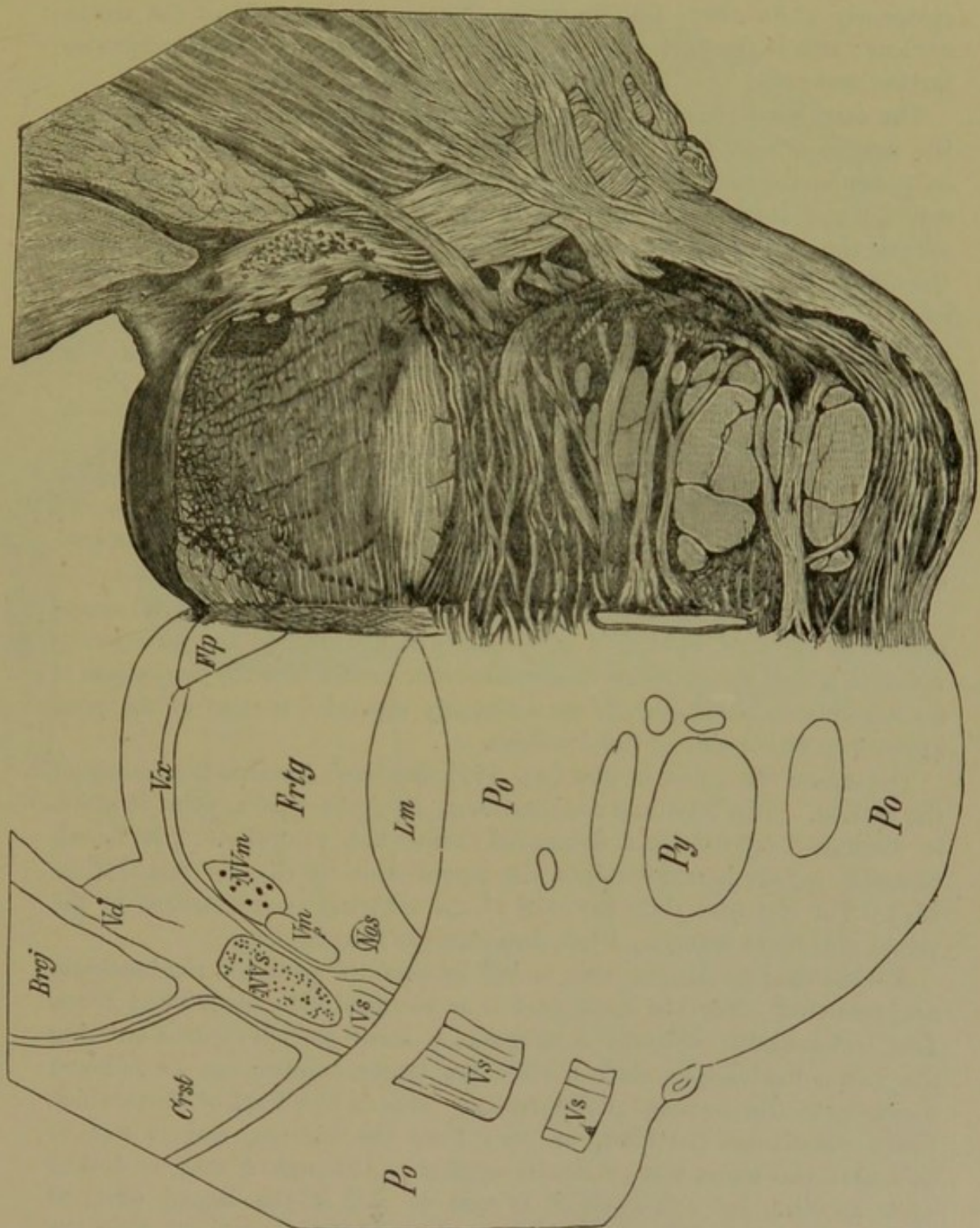


Fig. 143.—Transverse section, fig. 131 *m*.—*Brdj*, Brachium conjunctivum; *Vd*, cerebral root of trigeminus; *Vx*, crossed root of trigeminus; *NVs*, sensory trigeminal nucleus; *Vs*, sensory trigeminal root; *NVm*, motor trigeminal nucleus; *Vm*, motor trigeminal root; *Nos*, cerebral end of upper olive; *Frtg*, tegment.

On the mesial side of the sensory nucleus lies a compact roundish group of large nerve-cells, *NVm*, the motor nucleus of the fifth nerve. From



between the two nuclei a tract of fibres can be followed which curves inwards towards the raphe, *Vx*; this belongs to the crossed origin of the trigeminus. A number of coarse fibres, seen in the section as a conspicuously white tract, *Vm*, lie up against the ventral pole of the motor nucleus; this is the part of the motor root of the nerve which originates farther forwards.

The trigeminus receives a further accession of fibres which come from the neighbourhood of the lateral angle of the ventricle. This bundle is only seen in the sections farther forwards; the cerebral (or, as it used to be called, descending) root of the trigeminus, *Vd*. At the lateral edge of the section the corpus restiforme is seen passing into the cerebellum; a great cross-cut field of fibres lies on its inner side, in the form of a curved club (the upper part of the club is cut away in fig. 143, but in fig. 144 the whole of it is seen). This is the brachium cerebelli ad cerebrum, *Brcj* (brachium conjunctivum, superior cerebellar peduncle), which passes forwards from the cerebellum, sinking into the tegmental region as soon as the trigeminal nerve makes room for it.

As soon as the facial and abducent nerves have disappeared, the portion of the section which lies between the raphe and the trigeminus (formatio reticularis tegmenti, or tegmental region) begins to be traversed by scattered arcuate fibres. In subsequent sections it rapidly diminishes in area.

Although in the following sections (figs. 144 to 146) the total cross-section of the pons is still of considerable size, owing to the direction in which it is cut, the entrance of the brachium pontis into the cerebellum is no longer seen, consequently no artificially separated portion of the pons appears on either side in the drawings.

The mesial fillet, *Lm*, is now (fig. 144) displaced towards the margin of the section. The brachium conjunctivum, *Brcj*, the ventral point of which is distinctly curved, has descended somewhat ventrally. The fourth ventricle is fast narrowing into the aquæductus Sylvii, *Aq* (figs. 145 to 148). For the first time the roof of the ventricle is represented by the velum medullare anterius, *Vlma*, carrying the lingula, *Lng*.

A somewhat triangular area is left between the pons and the brachium conjunctivum. For the most part it is occupied with medullated fibres, *Lml*, which course obliquely dorsalwards, a small portion of them entering the velum medullare anterius, while the larger number can be followed forwards to the corpora quadrigemina. This is the tract of fibres which really constitutes the fillet, as seen from the outside, and it was to this that the name was originally applied. Although it may be looked upon as fillet, *par excellence*, it is well to call it the lateral fillet, to distinguish it from the one which we have followed upwards from the spinal cord. To the latter we should now apply the name mesial fillet, *Lm*. Later on, it will be necessary to give some account of various confusing synonyms applied to its several parts.

Certain little groups of nerve-cells situated in this triangular cross-section of the fillet, and probably serving to give origin to some of its fibres (nuclei lemnisci lateralis, *Nlml*), deserve attention. Wedged in between the



brachium conjunctivum and fillet is another group of nerve-cells, to which *Kölliker* has given the name of nucleus tegmenti lateralis.

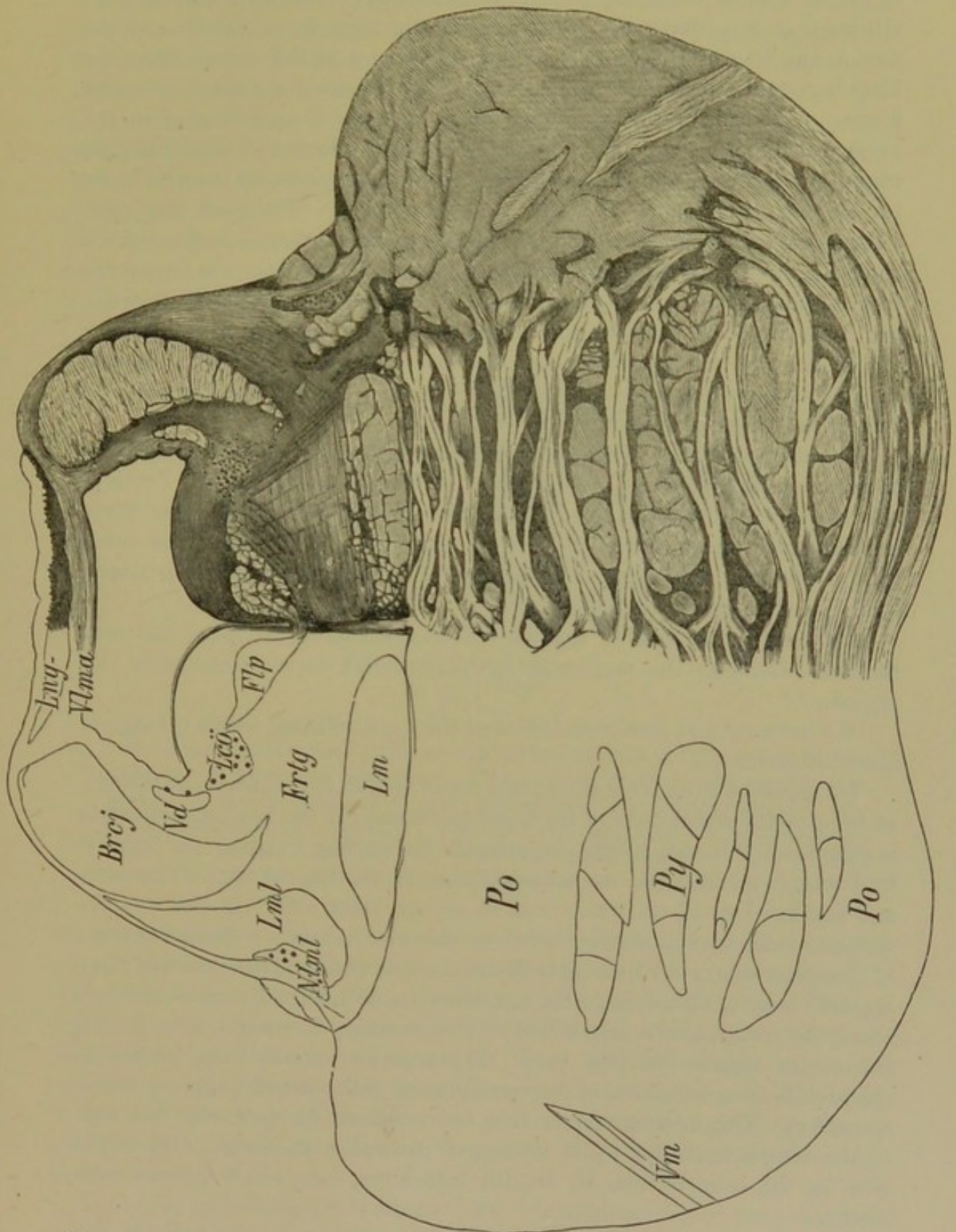


Fig. 144.—Transverse section, fig. 131 n.—*Vlma*, Velum medullare anterius; *Ling*, lingula; *Lcö*, locus cæruleus (substantia ferruginea); *Lml*, lateral fillet; *Nlm*, nucleus of lateral fillet; *Lm*, mesial fillet; *Vd*, cerebral root of trigeminus; *Vm*, motor root of trigeminus.



On the lateral side of the posterior longitudinal bundle lies a group of nerve-cells, which owing to its dark colour, dark enough to render it visible to the naked eye, is termed *substantia ferruginea, seu locus cœruleus, Lcö*; although it is perhaps better to restrict the term *locus cœruleus* to the area in the floor of the ventricle, which receives a bluish colour from the black *substantia ferruginea* which lies beneath it under a stratum of white fibres. [The cells of this group are easily recognised as belonging to the visceral column or 'vesicular column' of Clarke, by their well-filled outlines, round or oval form, and the small number of their processes, as well as by the closeness with which they are packed together. Wherever this intermittent column is present, whether in the sacral or dorsal regions of the cord, the nucleus of the vagus, or the *substantia ferruginea*, it is impossible to mistake it for groups of the motor cells of skeletal muscles.] Dorsally and laterally to the *substantia ferruginea*, always occupying the vicinity of the angle of the ventricle, a narrow tract of fibres, somewhat prolonged in the dorso-ventral direction, is cut across, *Vd*, the cerebral (descending) root of the trigeminal nerve.

The *fibræ arcuatæ* which traverse the tegmental region become sparser; they no longer pierce the mesial fillet. Owing to the increasing depth of the median fissure in the floor of the fourth ventricle, these arched fibres are constantly being driven farther ventralwards. The fibres of the motor root of the fifth, *Vm*, are still seen just before their exit from the lateral border of the pons.

Although a portion of the pons is still appended to them, the next sections belong to the mid-brain, for they exhibit nerves peculiar to this region.

We have not yet, however, described the **cerebellum**, which belongs to the hind-brain.

On account of the large size of this organ in Man it is convenient to make sections of the cerebellum of the monkey instead; if the human cerebellum is examined, it is well before preparing it for cutting frontally, to divide it by two sagittal sections, one corresponding to the lateral edge of the pons, and another 1 to 1½ cm. away from it, on the other side. In this way the central nuclei are completely shown on the one side and a sufficient amount of the other side is left to exhibit their relations and position. In this place we shall restrict ourselves to the consideration of a frontal section through about the centre of the cerebellum of the monkey, dividing it close behind the *corpus trapezoides* (fig. 145). The superior vermis, *Vrsp*, is seen in the middle line, a number of its convolutions being cut through one above the other. The inferior vermis does not reach so far forwards; the roof of the fourth ventricle, *V<sub>4</sub>*, is no longer covered with cortex. On either side lie the hemispheres, *H*, divided into lobes, everywhere covered with cortex.

Amongst the central masses of grey matter are seen—(1) in the vermis the considerable, somewhat wedge-shaped 'nucleus of the roof,' *Nt*, its angle almost reaching the middle line; (2) in the hemispheres the *corpora dentata cerebelli*, *Ndt* (*nuclei dentati, seu corpora rhomboidea*),



with their hila directed ventrally and mesially. Nucleus globosus and nucleus emboliformis (of Man) are not markedly developed.

Among the tracts of white fibres certain bundles which lie dorsally to the nuclei of the roof and cross one another in the middle line, taking part in the formation of the great commissure, *Co +*, are especially conspicuous. Certain of these fibres, however, dip down in the middle line between the roof nuclei and form a kind of raphe. They probably run in a sagittal direction (brain- or spinewards) after crossing. Strongly marked concentric arches of medullated fibres are very distinctly seen on the outer sides of the corpora dentata.

If we commence our description of the mid-brain with fig. 146, it is because the section shows the origin of the trochlear nerve, *IV*. Its fibres are seen distinctly crossing their fellows from the opposite side in the roof

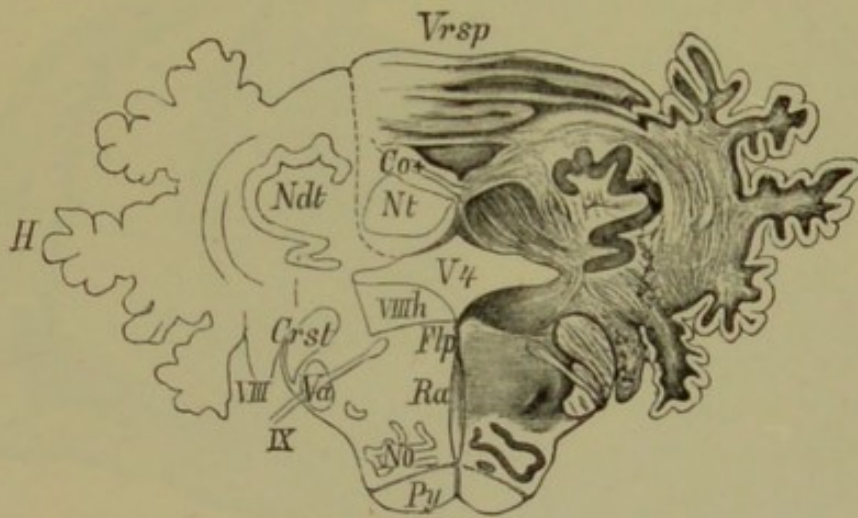


Fig. 145.—Frontal section through the cerebellum and medulla oblongata of a monkey. *Magn. 2.*—*H*, Cerebellar hemisphere; *Vrsp*, vermis superior; *Ndt*, nucleus dentatus; *Nt*, nucleus tecti; *Co +*, great commissure; *V<sub>4</sub>*, fourth ventricle; *Crst*, corpus restiforme; *Py*, pyramid; *Flp*, fasciculus longitudinalis posterior; *Ra*, raphe; *No*, nucleus olivaris; *VIII*, nervus acusticus; *VIIIh*, chief auditory nucleus; *IX*, nervus glossopharyngeus; *Va*, spinal root of trigeminus.

of the aquæductus Sylvii. Certain bundles of fibres lying on the inner side of the descending root of the fifth are cut transversely or obliquely, *IV*<sup>1</sup>. These are the root-fibres of the trochlear nerve which have their nuclei of origin farther brainwards. On the dorsal side of the posterior longitudinal bundle, close to the raphe, lies a striking darkly coloured rounded group of the smallest cells, which has been erroneously supposed to give origin to fibres of the trochlear nerve. It is the so-called posterior nucleus of the trochlear nerve or Westphal's nucleus (not lettered in the figure).

The recognised (anterior) nucleus of the trochlear nerve lies immediately to the cerebral side of this group of cells. [If, as in all probability may safely be done, we accept pigmentation and shrinkage in size as evidence of atrophy, and look upon groups of strongly pigmented cells as the vestiges of nuclei no longer functional, this group may possibly represent



the nucleus of an additional portion of the trochlear nerve, which there are good grounds for believing existed in early vertebrates. Both the third and fourth nerves take origin from spots in the mid-brain which contain deeply-pigmented cells, and both contain, mixed up with their nerve-fibres, masses of tissue which occur in no other nerves, but have all the characters of atrophied nerve-cells and cell-sheaths (*Thomson*), and may well be, as *Gaskell* believes, the vestiges of root-ganglia. Apart from these indications within the nerves and their nuclei, there are many reasons for thinking that the third and fourth nerves, which in all, or almost all, vertebrates are limited to fibres supplying certain muscles of the eye, had, before the

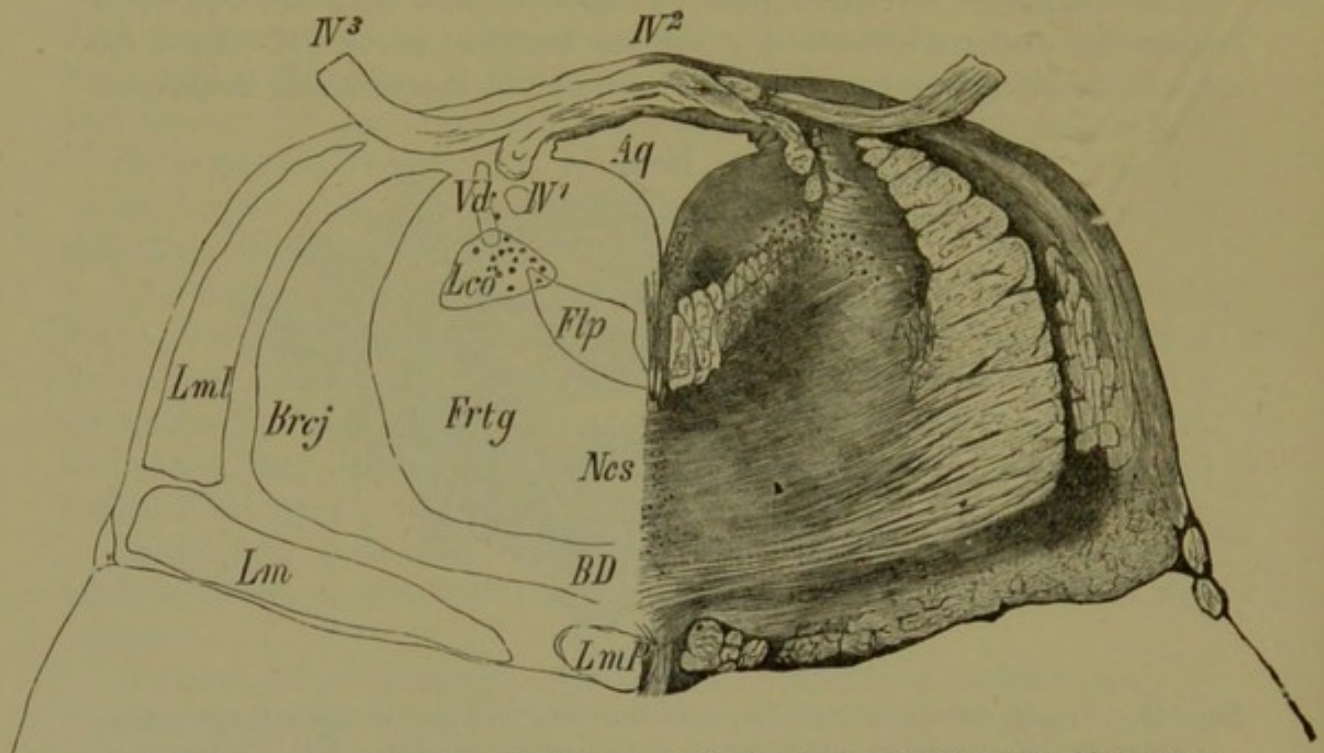


Fig. 146.—Transverse section, fig. 131 o.—*IV¹*, Cerebral root of the trochlear nerve; *IV²*, trochlear decussation; *IV³*, issuing root of n. trochlearis; *Aq*, aquæductus Sylvii; *Ncs*, nucleus centralis superior; *LmP*, bundle from fillet to crusta; *BD*, commencing decussation of brachia conjunctiva.

consolidation of the vertebrate head, a wider range, and included sensory as well as motor elements.]

Laterally and ventrally to the aqueduct the cerebral root of the fifth, *Vd*, the locus coeruleus, *Lcö*, and the posterior longitudinal bundle, *Flp*, retain the same relative position as heretofore. The lateral fillet, *Lml*, lies on the outer side of the brachium conjunctivum, *Brcj*, the ventral limb of the cross-section of which joins the main body almost at a right angle. The two are separated by a thin line of grey substance, the nucleus lateralis tegmenti. The ventral division of its fibres already reaches the middle line forming the commencement of the decussation of the brachia conjunctiva, *BD*. The tendency of the brachia towards the middle line is seen in the following sections, while the mesial fillet, *Lm*, inclines in the opposite direction, away from the raphe. Only the most mesial of its fibres remain behind in a rounded bundle lying dorsally to the pons, *LmP*. The nerve-



cells which are seen near the raphe, between the posterior longitudinal bundles and the decussation of the brachia conjunctiva, are here called the nucleus centralis superior, *Ncs*. The two bundles of fibres, cut across on the periphery between the fillet and the pons, constitute the ponticulus.

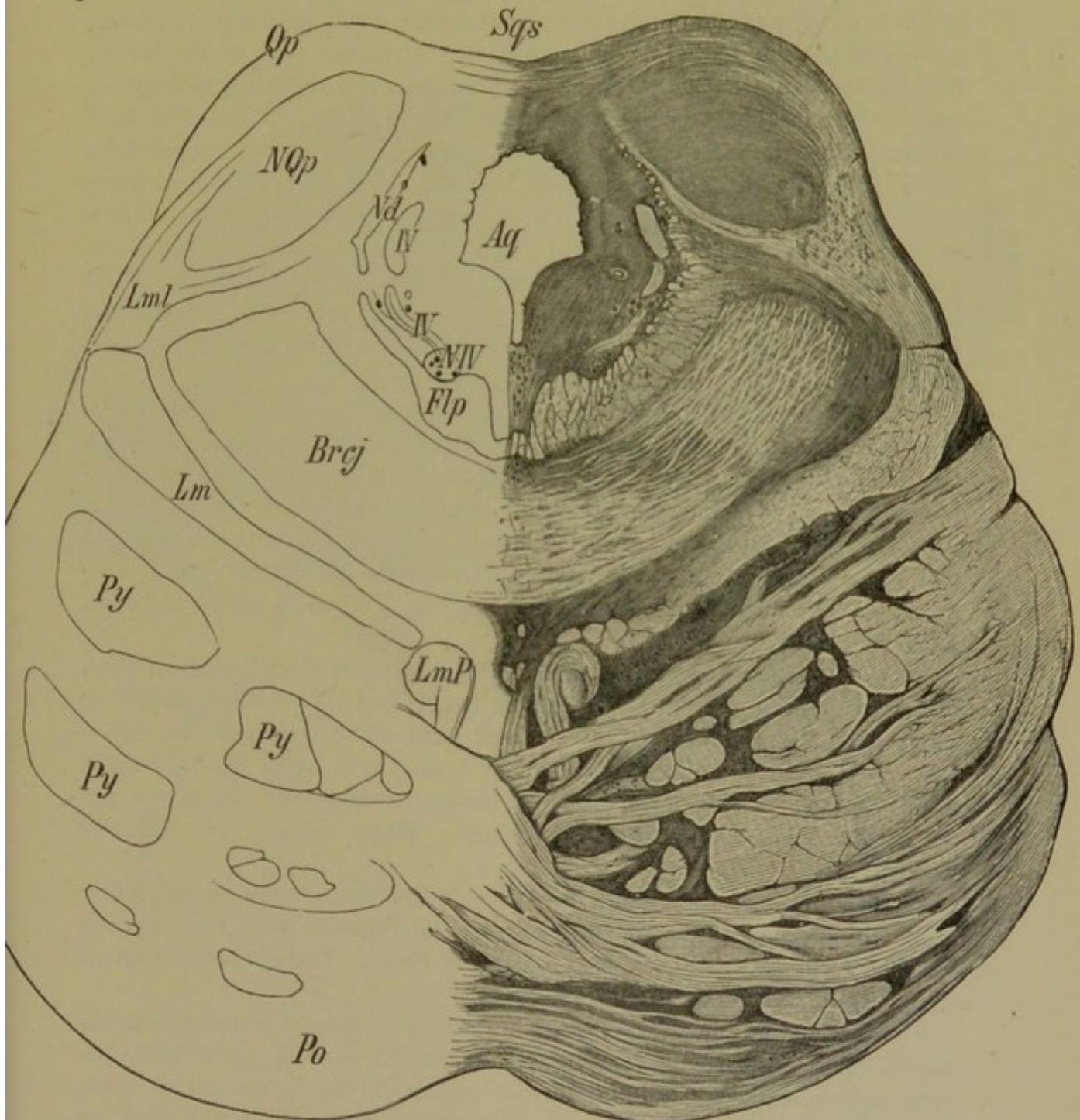


Fig. 147.—Transverse section, fig. 131 p.—*Qp*, Posterior corpora quadrigemina; *NQp*, nucleus of *ditto*; *NIV*, trochlear nucleus; *Sqs*, sulcus corporum quadrigeminorum longitudinalis.

The fibres of the trochlear nerve take origin in large part, as the following sections show, from a rounded grey mass, the (anterior) nucleus of the trochlear nerve, *NIV*, which in part is embedded in a concavity on the dorsal side of the posterior longitudinal bundle. Now for the first time the



posterior corpora quadrigemina, *Qp*, are seen in section, their united portions bridging over in the middle line the aquæductus Sylvii, *Aq*, which is prolonged into a deep channel on the ventral side. The centre of each lobe of the corpora quadrigemina is occupied by an ill-defined grey mass, the nucleus of the posterior corpora quadrigemina, *NQp*. On the outer side of this is recognised the bundle of the lateral fillet, *Lml*; part being, perhaps, prolonged to the middle line and across it. A smaller part of the lateral fillet passes beneath the nucleus of the corpora quadrigemina, so that the grey matter is almost completely encapsuled in white. The mesial fillet continues its course laterally and dorsalwards. The brachia conjunctiva, *Brcj*, enter to a greater extent into their decussation, and moving downwards come to occupy apparently the greater part of the formatio reticularis of the tegment. The pons fibres, *Po*, have split the pyramid, *Py*, into a great number of separate bundles; but, nevertheless, we find the pyramids in the sections just in front of the pons condensed into an immense close-set field of fibres, presenting a cross-section convex on its ventral side, *Pp* (pes pedunculi, [crusta]).

Fig. 148 represents a section carried through the hinder part of the anterior corpora quadrigemina, *Qa*. A superficial indentation is seen in the middle of its dorso-lateral border, *Sqt*; this is the fissure (sulcus inter-brachialis) which bounds the brachium corporis quadrigemini posterioris on its dorsal side, and it shows us, therefore, that we have passed the posterior and entered the region of the anterior tubercles of the corpora quadrigemina. The nucleus of the anterior tubercle is already visible although indistinct, *NQa*.

Between the pes pedunculi and the now no longer sharply-defined fillet, an ever enlarging grey mass insinuates itself, *SnS*; it is distinguished by possessing strongly pigmented cells, and assumes, therefore, to the naked eye a characteristic dark grey colour (substantia nigra Soemmeringi). Many bundles of fibres are seen to stream horizontally from the pes pedunculi into the substantia nigra. They cannot be followed farther.

On either side of the middle line, the brachia conjunctiva, beyond their main decussation, begin to form an oval field placed with its long axis vertically (the white nucleus of the tegment *Brcj*). These tracts of crossed fibres are reinforced by those still crossing.

The rounded bundles, *LmP*, which we had noticed as separating from the mesial fillet, place themselves, as soon as the fibres of the pons have disappeared, on the mesial side of the pes pedunculi, on the margin of which they soon spread out sideways. Hence they constitute the tracts from the fillet to the pes.

The space between the posterior longitudinal bundles and the aqueduct of Sylvius has considerably increased in its dorso-ventral diameter. It is occupied by a region rich in cells, the ventral part of which belongs, as later sections will show, to the nervus oculomotorius, *NIII*.

The large brown cells of the substantia ferruginea have completely disappeared, and the cerebral root of the fifth, *Vd*, is only picked out with



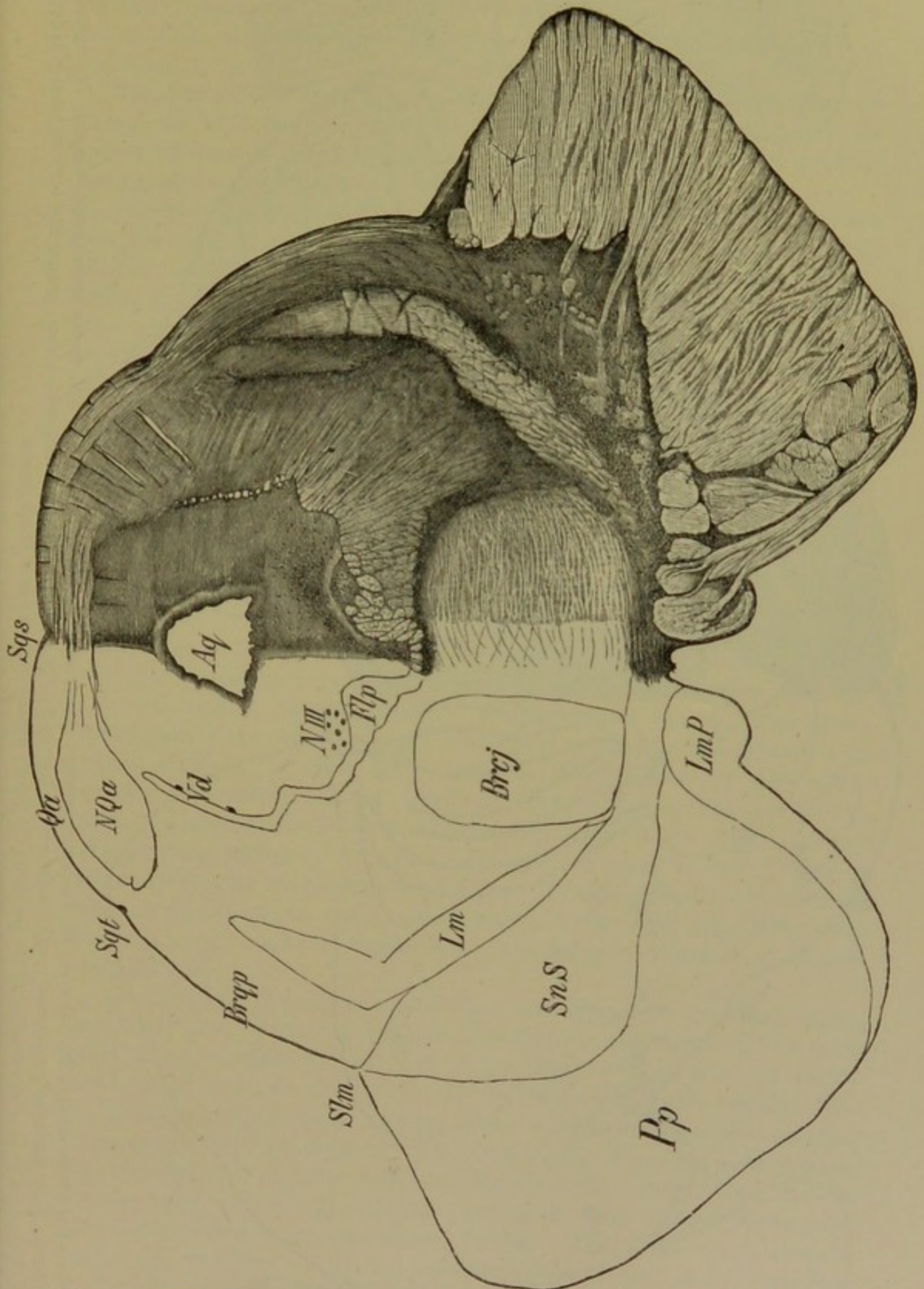


Fig. 148.—Transverse section, fig. 131 *q*.—*Qa*, Anterior corpora quadrigemina; *Nqa*, nucleus of *ditto*; *Sqt*, sulcus corpor. quadrigem. transversus; *Brqp*, brachium corporis quadrigemini posterioris; *Slm*, sulcus longitudinalis mesencephali; *NIII*, nucleus of nervus oculomotorius; *SnS*, substantia nigra Soemmeringi; *Pp*, pes pedunculi.



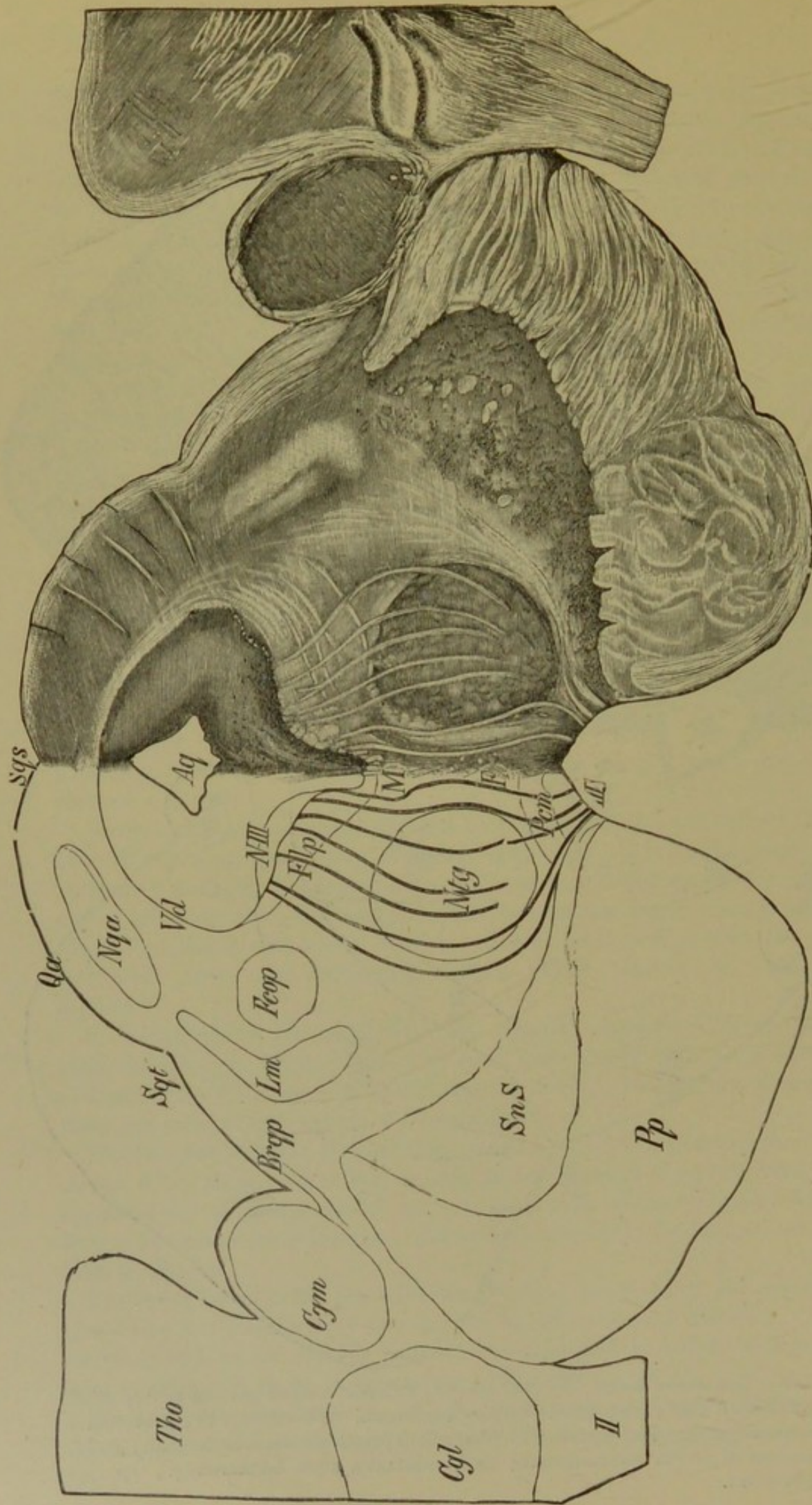


Fig. 149.—Transverse section, fig. 131 r.—*Tho*, Thalamus opticus; *Cgm*, corpus geniculatum mediale; *Cgl*, corpus geniculatum laterale; *II*, tractus opticus; *Fcp*, posterior commissure; *Ntg*, nucleus ruber tegmenti; *III*, root fibres of n. oculomotorius; *Pcm*, pedunculus corporis mammillaris; *M*, Meynert's fontanal decussation of the tegment; *F*, Forel's ventral decussation of the tegment.



difficulty under a low power; it can still be recognised, however, if one relies upon the scanty but very characteristic large nerve-cells which it contains.

The fibres which cross dorsally to the aqueduct are very conspicuous. They can be followed farther to each side, the most ventrally situate sweeping down in a well-formed arch towards the cerebral root of the fifth, as appears more clearly in the following sections.

A section carried through the summit of the anterior tubercles of the corpora quadrigemina show certain well-marked changes (fig. 149). The sulcus corporum quadrigeminae sagittalis, *Sqs*, is deep and well defined; while the sulcus interbrachialis, which separates the anterior tubercle from the brachium of the posterior tubercle, seems to have inclined farther ventralwards, *Sqt*. Many medullated fibres cross the middle line dorsally to the aqueduct of Sylvius.

The crossing of the brachia conjunctiva is complete, and instead of the brachia themselves a round area, formed of reticular substance, into which the fibres have passed, occupies their place on the dorsal side of the substantia nigra and not far from the middle line. This is the red nucleus, *Ntg* (superior olive of *Luys*, nucleus tegmenti).

On the dorsal side of the posterior longitudinal bundle, large nerve-cells are seen, *NIII* (nucleus nervi oculomotorii). They give origin to bundles of fibres which sweep ventrally, first piercing the posterior longitudinal bundle; some pass on the inner side, some on the outer side, and others through the red nucleus to reach the surface at the furrow between the two crura cerebri, *III* (root-fibres of the oculomotor nerve). This group forms part of the region in which the nervus oculomotorius originates—its lateral nucleus. In other large cells on either side of the middle line we find its central nucleus, and dorsally from the lateral nucleus lie numerous small cells which constitute the nucleus nervi oculomotorii of *Westphal* and *Edinger*. All these cells together must be looked upon as the starting-point of the oculomotor fibres. Ventrally to the red nuclei the fibres of the oculomotor nerve pass through a region, *Pcm*, occupied by fibres running from the corpus mammillare to the tegment (pedunculus corporis mammillaris).

The distinctly diminished mesial fillet, *Lm*, appears as an inconspicuous, semilunar area, stretching towards the corpora quadrigemina. It takes part in the crossing in the roof of the aqueduct. A hardly recognisable patch, *Fcop*, on the mesial side of the fillet, which remains light in carmine preparations, contains fibres streaming from the posterior commissure into the tegment (*Wernicke*). Fine fibres are seen crossing in the raphe from the level of the posterior longitudinal bundles to the basis cerebri. The dorsal portion of these crossing fibres must be distinguished from the ventral (*Forel*). The fibres which cross in the dorsal segment of the raphe come from the roof of the aqueduct; principally, indeed, from the anterior corpora quadrigemina; sweeping in fine curves around the outer side of the cerebral root of the fifth, they curl in beneath the posterior longitudinal bundle, and so traverse the



tegment towards the middle line. *Meynert*, thinking that these fibres take origin in the cells of the cerebral trigeminal root, called them the tracts of the fifth (Quintusstränge). *Forel* substituted the name 'fountain-like or Meynert's decussation,' *M*. The fibres which cross in the ventral portion of the raphe form *Forel's* ventral tegmental decussation, *F*.

The most remarkable feature of this section is the fact that a large number of new structures, most of which are connected with the optic nerve, are found on its lateral borders. A great white column cut obliquely lies up against the crusta, the tractus opticus, *II*. Dorsally it passes into a peculiar mass of alternating grey and white matter, the ganglion or corpus geniculatum laterale, *Cgl*. A smaller part of the optic fibres can be followed on the surface of the crusta farther dorsally to another grey body of oval form and almost the same size as the nucleus ruber tegmenti, the ganglion, *seu* corpus geniculatum mediale, *Cgm*. The mesial geniculate body is situate in the sulcus lateralis mesencephali; it is enveloped all over in bundles of fibres, and gives some bundles to the corpus quadrigeminum posterius. Lastly, the section has already cut into the thalamus opticus, *Tho*, which appears as a great grey mass lying on the dorsal and lateral sides of the structures described above.

Still another section must be made through the anterior border of the corpus quadrigeminum anterius, so that it cuts the posterior commissure, *Cop* (fig. 150). By this time the optic thalamus occupies an extended area. Each of the anterior corpora quadrigemina is united with the thalamus by a conspicuous arched tract of white fibres, the brachium corporis quadrigemini anterioris, *Brqa*, which lies in the furrow between them. The considerable tracts of the posterior commissure cross above the aqueduct (already opening out into the third ventricle); their most ventral fibres extend downwards on either side the aqueduct in the direction of the posterior longitudinal bundles, *Flp*, which are already indistinct. The dorsal fibres of the commissure, separated from the ventral fibres by the recessus subpinealis, *Rsp*, can be followed farther sideways into the thalamus. The most anterior portion of the nucleus oculomotorius, *NIII*, is still to be seen near the raphe.

Fibres stream outwards from the lateral edges of the red nuclei, *Ntg*. Many bundles of fibres belonging to the thalamus take a similar course in the most lateral part of the section. The substantia nigra Soemmeringi, *SnS*, has disappeared with the exception of a little mesial portion. Its place is taken by a lenticular body, the corpus subthalamicum, *Csth*, which, as we shall see later on, ought to be apportioned to the 'tween-brain. It is surrounded by a white capsule. The two corpora mammillaria, *Cm*, are squeezed in between the crura cerebri beneath the substantia perforata posterior, *Sbpp*.

On the mesial side of the red nucleus lies a region, *Al*, rich in fibres belonging to the ansa lenticularis.

Dorsally it is not well marked off from the field of cross-cut fibres which lies on the ventral side of the posterior longitudinal bundle. A tract of coarse fibres, the fasciculus retroflexus, *frtf* (*Meynert's* bundle), discharges



in this region. It enters into the nucleus ruber on its inner side. Its commencement and termination are not visible in this section.

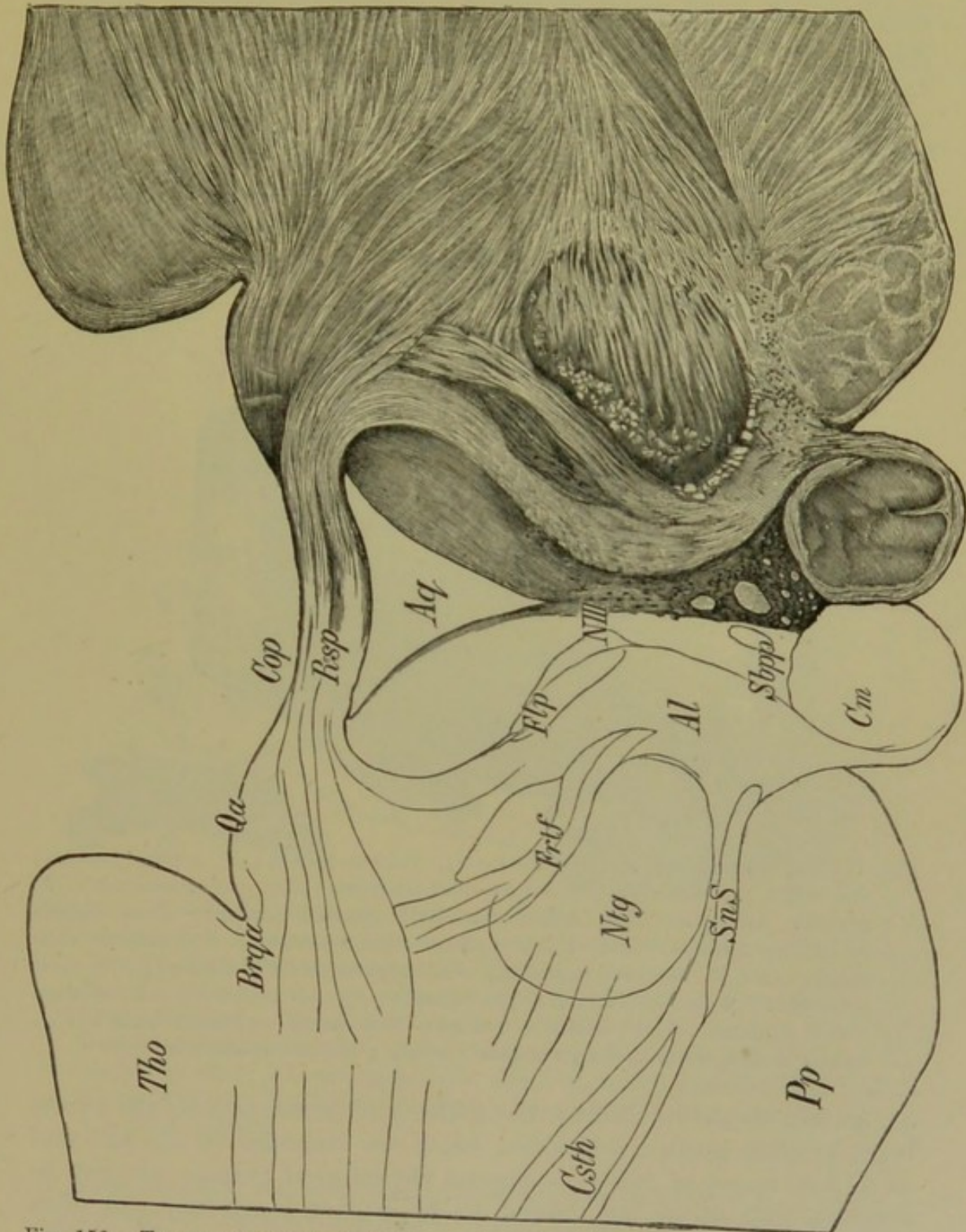


Fig. 150.—Transverse section, fig. 131 s.—*Cop*, Commissura posterior; *Rsp*, recessus subpinealis; *Brqa*, brachium corporis quadrigemini anterioris; *Qa*, front of anterior corpus quadrigeminum; *Aq*, aquæductus Sylvii where it opens into third ventricle; *Frtf*, fasciculus retroflexus; *Csth*, corpus subthalamicum; *Flp*, posterior longitudinal bundle; *Al*, ansa lenticularis; *Sbpp*, substantia perforata posterior; *Cm*, corpus mammillare; *SnS*, anterior end of substantia nigra Soemmeringi; *Ntg*, red nucleus and fibres streaming from it; *Pp*, pes pedunculi cerebri.



In the foregoing sections we found it advisable to cut away the lateral parts of the brain before hardening, lest the preparations should be inconveniently large. This proceeding is even more necessary in making sections of the brain-stem when it lies beneath the central part of the hemispheres. The next three preparations, which are intended to serve for the explanation of the 'tween-brain and secondary fore-brain, are consequently incomplete; but the parts cut away present no feature which it is essential to reproduce.

I must also point out that, while the carmine preparations were magnified to four times their natural size, these, which are stained by Pal's method, are only twice the natural size.

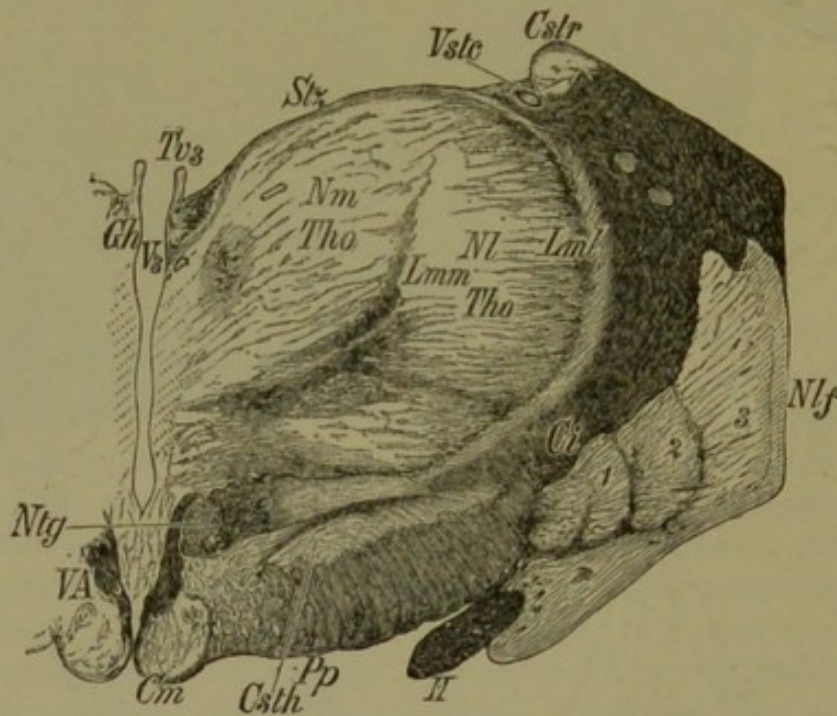


Fig. 151.—Transverse section, fig. 133 *t.*—*II*, Tractus opticus; *Ci*, capsula interna; *Cm*, corpus mammillare; *Csth*, corpus subthalamicum; *Cstr*, corpus striatum; *Gh*, ganglion habenulae; *Lml*, lamina medullaris lateralis thalami; *Lmm*, lamina medullaris medialis thalami; *Nl*, nucleus lateralis thalami; *Nlf*, nucleus lentiformis; 1, 2, 3, its three segments; *Nm*, nucleus medialis thalami; *Ntg*, most anterior end of the red nucleus of the tegment; *Pp*, pes pedunculi; *Stz*, stratum zonale thalami; *Tho*, thalamus opticus; *Tv3*, taenia ventriculi tertii; *VA*, bundle of Vicq d'Azyr; *Vstc*, vena strie corneae; *V3*, third ventricle.

As will be shown directly, the anatomy of certain parts of the 'tween-brain presents peculiar difficulties, which are increased by the fact that to certain tracts of fibres no distinct physiological purpose can yet be assigned, and so we are obliged to be contented with dry and often doubtful anatomical data. The very existence of the tracts in question is sometimes rather taken for granted than demonstrated. In fact, the gaps in our information so often felt in the study of many parts of the brain are experienced acutely in the case of the 'tween brain.

A section carried in front of the posterior commissure (fig. 151) shows us structures with most of which we are already acquainted.

The aqueduct of Sylvius is fully enlarged into the third ventricle, *V3*.



The optic thalamus shows us its two free surfaces, the mesial looking into the third ventricle. The edge between the two surfaces is marked by a little swelling, the ganglion habenulæ, *Gh*, from which the tænia ventriculi tertii originates. In a somewhat earlier section we should have seen the fasciculus retroflexus extending downwards from the ganglion habenulæ. The corpora mammillaria lie beneath the substantia perforata posterior, *Slpp*.

From either side a large and conspicuous bundle of medullated fibres passes dorsalwards into the thalamus. This is the bundle of Vicq d'Azyr, *VA*.

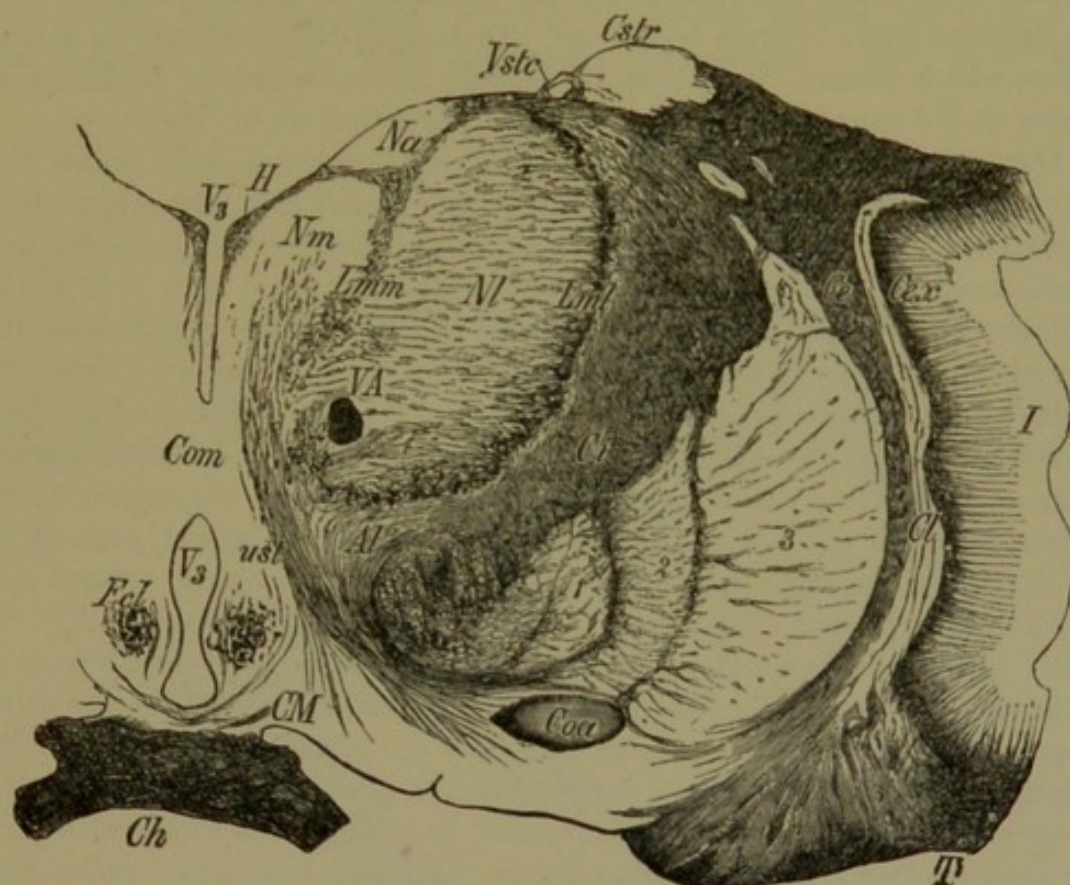


Fig. 152.—Transverse section, fig. 133 *u*.—1, 2, 3, The three segments of the nucleus lenticularis; *Al*, ansa lenticularis; *Ce*, capsula externa; *Cex*, capsula extrema; *Ch*, chiasma nervorum opti-; *Ci*, capsula interna; *Cl*, claustrum; *CM*, Meynert's commissure; *Coa*, commissura anterior; *Com*, commissura media; *Cstr*, corpus striatum; *Fcl*, columna fornix; *H*, habenula; *I*, island of Reil; *Lml*, lamina medullaris lateralis; *Lmm*, lamina medullaris medialis thalami; *Na*, nucleus anterior; *Nl*, nucleus lateralis, and *Nm*, nucleus medialis thalami optici; *T*, temporal lobe; *ust*, inferior peduncle of the thalamus; *Vstc*, vena strie corneae; *V3*, third ventricle.

In its subsequent course towards the anterior nucleus thalami it assumes a more sagittal direction, and will be visible in later sections as a roundish tract of transversely cut fibres.

The lamina medullaris medius, *Lmm*, divides the thalamus into two parts, the smaller of which is the mesial nucleus, *Nm*, and the larger the lateral nucleus, *Nl*. In the woodcut we also see that the lamina medullaris medius itself is divided into two parts, enclosing a little grey substance between them. In sections taken somewhat farther back this grey space would be seen as a fairly large, roundish body, sharply defined by the



medullated fibres of the lamina medullaris. It is the "centre médian" of *Luys* (the middle nucleus of *Kölliker*). The hinder part of the lateral nucleus passes over into the pulvinar. From the outer side numerous white fasciculi press into it, giving to it for a certain thickness a peculiar reticulate appearance, the stratum reticulatum, *str.* On the lateral border of the thalamus these fibres are collected into a thin boundary layer, the lamina medullaris lateralis, *Lml.* On the outer side of this comes the internal capsule, *ci*, into which the crus cerebri enters from below.

Not everything, however, which lies between the internal capsule and the third ventricle belongs to the optic thalamus; the basal portion of the region, which cannot, it is true, be sharply defined from the thalamus, is known as the regio subthalamica (stratum intermedium of *Wernicke*).

Our attention is arrested by a somewhat lenticular body which lies above the internal capsule and towards its mesial side, the corpus subthalamicum, *Csth* (nucleus amygdaliformis, nucleus of *Luys*, nucleus of *Forel*, bandelette accessoire de l'olive supérieure). In Man it is much more sharply defined than in many animals. The corpus subthalamicum is, with the single exception of its mesial angle, shut in by a thin but distinct capsule of medullated fibres, capsula corporis subthalamici. The ventral lamella of its capsule separates it from the crus, or internal capsule, as the case may be; the dorsal lamella separates it from the region which is in connection dorso-laterally with the fibres of the lateral nucleus of the thalamus, the regio subthalamica proper, and gains on the ventral and mesial side a greater importance by blending with the region *Ntg*, in which we must look for the fibres which stream out of the dorsal portion of the red nucleus. This area is continued almost to the wall of the third ventricle, but it must be pointed out that our views with regard to its definition are by no means concise. *Monakow* gives the name of "ventral group of nuclei of the thalamus opticus" to a large area which, although not always clearly defined, especially on its dorsal boundary towards the actual lateral nucleus, is distinguishable even on microscopic examination by the different disposition of the elements which compose it. Within this area he again distinguished four separate nuclei. *Forel* distinguishes the ventral portion of this area which lies next to the corpus subthalamicum (zona incerta) from the upper more abundantly medullated one.

Above the thalamus opticus in fig. 152 we see the stria cornea with its large vein (*Vstc*). Farther to the side is the tail of the nucleus caudatus (*Cstr*).

Last, the tractus opticus (*II*) remains to be mentioned. It lies close against the pes pedunculi cerebri.

The next woodcut (fig. 153) shows the thalamus and the nucleus lenticularis in their greatest extension. At the outside of the latter are seen the capsula externa (*Ce*), the claustrum (*Cl*), the capsula extrema (*Cex*), and the cortex of the insula.

In the thalamus opticus we see the two laminæ medullares, *Lml* and *Lmm*. The lamina medullaris medialis divides it into a lateral and a mesial nucleus (*Ne* and *Nm*); and the anterior nucleus (*Na*) begins to be distinctly



defined. The bundle of Vicq d'Azyr can be seen as a round patch cut across in the lateral nucleus.

Ventrally from the nucleus lenticularis we see the cross-section of the anterior commissure, which here passes obliquely backwards, turning at right angles to the middle line farther on. Further, on the ventral side of both the inner segments of the nucleus, we meet with numerous fibres which pass towards the middle line and arch upwards on reaching the apex of the nucleus, and so curve round the ventral end of the inner capsule and stream into the region included under the general name of regio subthalamica. These form the ansa lenticularis. The name ansa

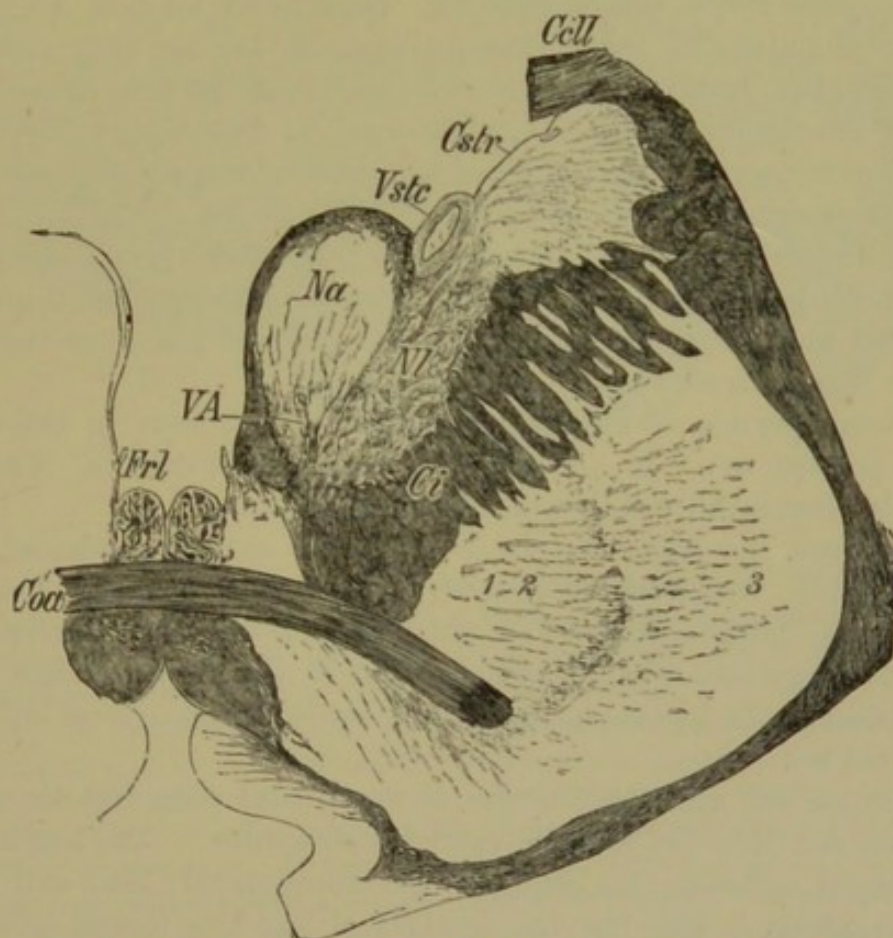


Fig. 153.—Transverse section, fig. 133 v.—1, 2, 3, The three segments of the nucleus lenticularis; *Cell*, corpus callosum; *Coa*, commissura anterior; *Cstr*, corpus striatum; *Frl*, columna fornicis; *Na*, nucleus anterior; *NL*, nucleus lateralis thalami; *VA*, bundle of Vicq d'Azyr; *Vstc*, vena striæ cornæ.

peduncularis is applied to all fibres which curve round the internal capsule (and the pes pedunculi) at this point. Its two most important constituents are the ansa lenticularis just described, and a second fibre tract, which streams upwards between the bundle of Vicq d'Azyr and the columna fornicis (*Fcl*), into the mesial and anterior nuclei of the thalamus. These fibres constitute the inferior peduncle of the thalamus, *ust* (inferior or inner peduncle of *Wernicke* and *Meynert*). Possibly its fibres take origin in the two inner segments of the nucleus lenticularis. It is certain, however, that other fibres derived from the ventral side of these two segments of the nucleus lenticularis, always more numerous than those



just described, have a different destination ; the cortex of the temporal lobe, for example.

On the base of the brain lies the optic chiasm, *Ch* (chiasma nervorum opticom), above which, in the narrow interval between it and the third ventricle, run certain fasciculi of thick fibres forming Meynert's commissure, *Com*. Besides these, other and finer fibres cross here and strike upwards towards the thalamus opticus. These constitute Forel's decussation.

The middle commissure (*Com*) divides the third ventricle into two parts, lying one above the other.

In the next figure the thalamus opticus has been to a great extent displaced by the corpus striatum (*Cstr*). The anterior nucleus, *Na*, and the stratum reticulatum of the lateral nucleus, *Nl*, are the only parts of it still discernible. In the anterior nucleus the bundle of Vicq d'Azyr is seen to enter ; the inner capsule, *Ci*, is traversed by numerous bridges which connect the corpus striatum and nucleus lenticularis, and extend even to its outer segment, the putamen (*S*).

The putamen is continued towards the base of the brain without any sharp line of demarcation. The most conspicuous feature of this section is the great anterior commissure (*Coa*), to which the pillars of the fornix (*Frl*) are seen affixed.

The small portion of the corpus callosum (*ccl*) seen in this section must be pointed out. It lies above the nucleus caudatus. The great mass of the corpus callosum has already been cut away.

In more anterior segments the head of the nucleus caudatus will be found to have completely displaced the optic thalamus. The third segment of the nucleus lenticularis alone keeps it company, the two being connected by numerous wide bridges. From the lower surface of the corpus callosum the septum pellucidum extends downwards on either side the middle line.

If sections are made still nearer to the frontal pole, first the nucleus lenticularis and then the nucleus caudatus disappears. The bending over of the corpus callosum (its genu) is next encountered ; and still farther forwards nothing is left but the sections of the two frontal lobes, now completely separated from one another.

The student will find it of the greatest service to survey the various fibre-tracts, cell-groups, etc., which he has learnt to know in the foregoing series of cross-sections, from another point of view. The comprehension of the brain as a whole is greatly aided by the preparation of sections taken in different planes. It is well to study a series cut parallel with the mesial plane.

For this purpose we must take a well-hardened brain-stem, extending about as far forwards as the anterior commissure, and cut away part of one side, parallel to the mesial plane and about a centimeter or a centimeter and a half from the middle line. The cut surface will serve as a



base for fixing the preparation on to the cork or wooden block after it has been properly embedded in celloidin. The projecting medulla oblongata, which forms the caudal part of it, must be supported by filling in with photoxylin. Fig. 154 shows the relations of the parts as seen in such longitudinal sections; it is partly of the nature of a diagram, and combines

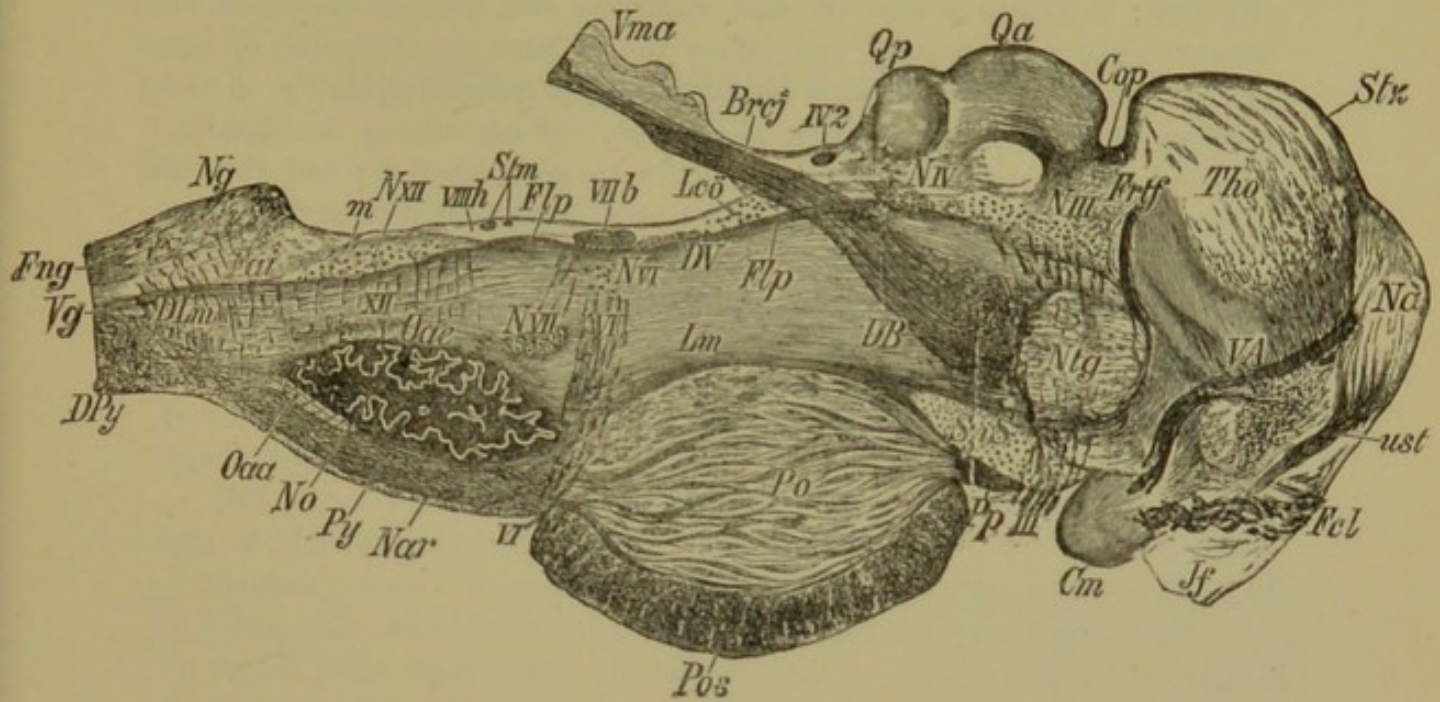


Fig. 154.—Combination of several sagittal sections through the brain-stem. *Pal's* staining. Magn. 2.—III, Nervus oculomotorius; IV2, decussation of the nervus trochlearis; VI, nervus abducens; VIIb, ascending limb of facialis; VIIbh, triangular auditory nucleus; XII, nervus hypoglossus; Brej, brachium conjunctivum; Cm, corpus mammillare; Cop, commissura posterior; DB, crossing of brachia conjunctiva; DLM, decussation of the fillet; DPy, decussation of the pyramids; DV, crossed bundle of the trigeminus; Fai, fibræ arcuatæ internæ; Fcl, columna fornicis; Fng, funiculus gracilis; Flp, fasciculus longitudinalis posterior; Frtf, fasciculus retroflexus; Jf, infundibulum; Lco, locus cæruleus; Lm, fillet; m, dorsal longitudinal bundle above the nucleus hypoglossi; Na, nucleus anterior of the optic thalamus; Nar, nucleus arcuatus; Ng, nucleus gracilis; No, nucleus of the olive; Ntg, nucleus tegmenti; NIII, nucleus oculomotorii; NIV, nucleus trochlearis; NVI, nucleus abducentis; NVII, nucleus facialis; NXII, nucleus hypoglossi; Oaa, anterior accessory olive; Oae, exterior accessory olive; Po, pons; Pos, superficial fibres of the pons; Pp, pes pedunculi; Py, pyramid; Qa, anterior corpus quadrigeminum; Qp, posterior corpus quadrigeminum; SnS, substantia nigra Soemmeringi; Stm, striæ medullares acustici; Stz, stratum zonale thalami; Tho, thalamus opticus; ust, inferior peduncle of the thalamus; VA, bundle of Vicq d'Azyr; Vg, ground-bundle of the anterior column; Vma, velum medullare anterius.—In order to avoid overcrowding the figure with letters, many details shown in it are not expressly marked; as, for example, the transversely cut crossing of the facialis (under VIIb), or the equally faint indication of the corpus trapezoides (where the bundle of the abducens pierces the fillet).

in a measure the details of several sections, all parallel to the mesial plane, but taken at distances varying from two to four millimeters from the middle line.



Basal sections, as we should call those made parallel to the base of the brain, are particularly troublesome to prepare.

This plane is very unsuitable for making sections of the mid-brain and hind-brain in Man; it is better to take the floor of the fourth ventricle as our starting-point and try to cut parallel with that. Even then it is very difficult to obtain a proper surface for fixing the preparation on to the cork; to secure a base of even moderate size, part of the brain substance has to be cut away, and either the corpora quadrigemina or some of the ventral structures must be sacrificed; it is hardly possible to make sections without filling in with photoxylin. If embedding in celloidin is resorted to, the celloidin may be allowed to get almost dry and then the lump containing the preparation may be cut out and shaped as desired.

If, however, the frontal sections and a series of sagittal sections have been well studied, the understanding of the basal series will present no great difficulty.



## SECTION VI.—COURSE OF FIBRES.

We have now at command a continuous series of cross-sections—and, perhaps, also of longitudinal and basal sections—of the central nervous system. Such a series of sections from the *filum terminale* to the front of the great brain affords material for the study of the course of fibres on the one hand and minute structural relations on the other; although hitherto our attention has been confined to the larger topographical changes which the cross-section shows.

But these series, even when unbroken, do not suffice for the explanation of the course of the several fibre-tracts.

In many cases it is impossible to follow a single fibre, or even a bundle of fibres, with absolute certainty section by section from beginning to end. To avoid false conclusions, we are forced to have recourse to various other methods of investigation. For instance, Flechsig's method of studying the successive stages of development of the myelin-sheath often enable us to follow easily the whole course of certain fibres which acquire it earlier than those about them.

It is superfluous to insist upon the importance of the revelations made by the degeneration-method, whether applied to secondary degeneration or what is known as *v. Gudden's*. It reflects great credit upon *Monakow* that he has developed *v. Gudden's* teaching and applied it systematically to the results of secondary degeneration in Man. In new-born animals, as we know (and with certain reservations the same holds good for adults), after severance of a nerve-fibre, secondary degeneration extends to and involves its cell of origin. We then know for certain that the fibre arises from the cell. If, on the contrary, we see that, after the severance of a bundle of fibres, the degeneration can, indeed, be followed to a group of cells, but affects, not the cells themselves, but the intervening tissue, we know that in this group we must look for the end of the bundle (*Monakow*).

But this method leads us a step farther. I have already pointed out that the degenerative process does not stop at the neuron directly injured, but may extend to another, structurally and functionally dependent on the first. This is especially the case in young persons. The process we observe in the fibre of this second neuron is, however, not Waller's degeneration, but a mere reduction in volume—simple atrophy. *Monakow* is of opinion that this atrophy of the second degree (or tertiary atrophy, as it may be called, to avoid confusion with 'secondary' degeneration)



may be explained by the lack of, or insufficient transference of, nervous impulses consequent upon the destruction of the first neuron. Want of functional activity induces partial atrophy of the second neuron or (in young subjects) arrests its growth.

Important disclosures concerning the origin, course, and end of a nerve-tract may be gathered from the method of impregnating with silver, by which (to give an instance) the course of the axis-cylinder process can be most clearly seen. At the same time it must be borne in mind that the axis-cylinder frequently bends round, so that the direction in which it leaves the cell by no means necessarily corresponds with that of its later course. In other kinds of cells, such as the pyramidal cells of the cortex, it takes at once the direction in which it proceeds for some distance. With regard to the collaterals which the silver-method renders visible in the embryo, I would again remind the reader that the utmost caution is necessary in transferring to the adult the conditions of this stage of development.

But, at any rate, it is only by the application of the various methods of investigation that the student can hope to arrive at independent conclusions with regard to the matters next to be considered.

It must, however, be remarked that it is not our intention to quote in this place all the fibre-paths which have been described, especially when their course is of but little importance.

## A. TRACTS IN THE SPINAL CORD.

**I. Pyramidal Tracts** (fig. 155).—We have learnt to recognise the lateral, *PyS*, and anterior pyramidal tracts, *PyV*, in the spinal cord.

These tracts are composed of long fibres, which can be followed brainwards into the pyramids and through the pons, on into the crus and inner capsule, and through this to the cortex of the great brain. As, however, it is in the cells of the cortex that they originate, we will begin our study of them from that end.

Throughout the cortex cerebri (fig. 155, *Co*) we find, as I shall presently show more fully, an immense number of pyramidal cells, which send out their axis-cylinder processes into the medulla of the hemisphere. The nerve-fibres, which farther down constitute the pyramidal tracts, take origin in these cells; but I must at once explain that the name 'pyramidal tract' has nothing to do with the pyramidal cells, but is due to the circumstances that the pyramids situate at the base of the medulla oblongata are composed of these fibres.

A large proportion of the fibres from the pyramidal cells (*c<sup>1</sup>-c<sup>4</sup>*) converge and traverse the centrum semiovale Vieussenii (maintaining, on the whole, their relative positions) to constitute the corona radiata. Of these we need only take into consideration those which thrust themselves between the central grey masses (the nucleus lenticularis on the one side and the nucleus caudatus and optic thalamus on the other), and thus constitute the internal capsule, *Ci*.



We know that the internal capsule (fig. 156) consists, in horizontal section, of an anterior segment, between the nucleus lenticularis and the nucleus caudatus, and a posterior segment, between the nucleus lenticularis and the optic thalamus. The two meet at the so-called 'knee' of the

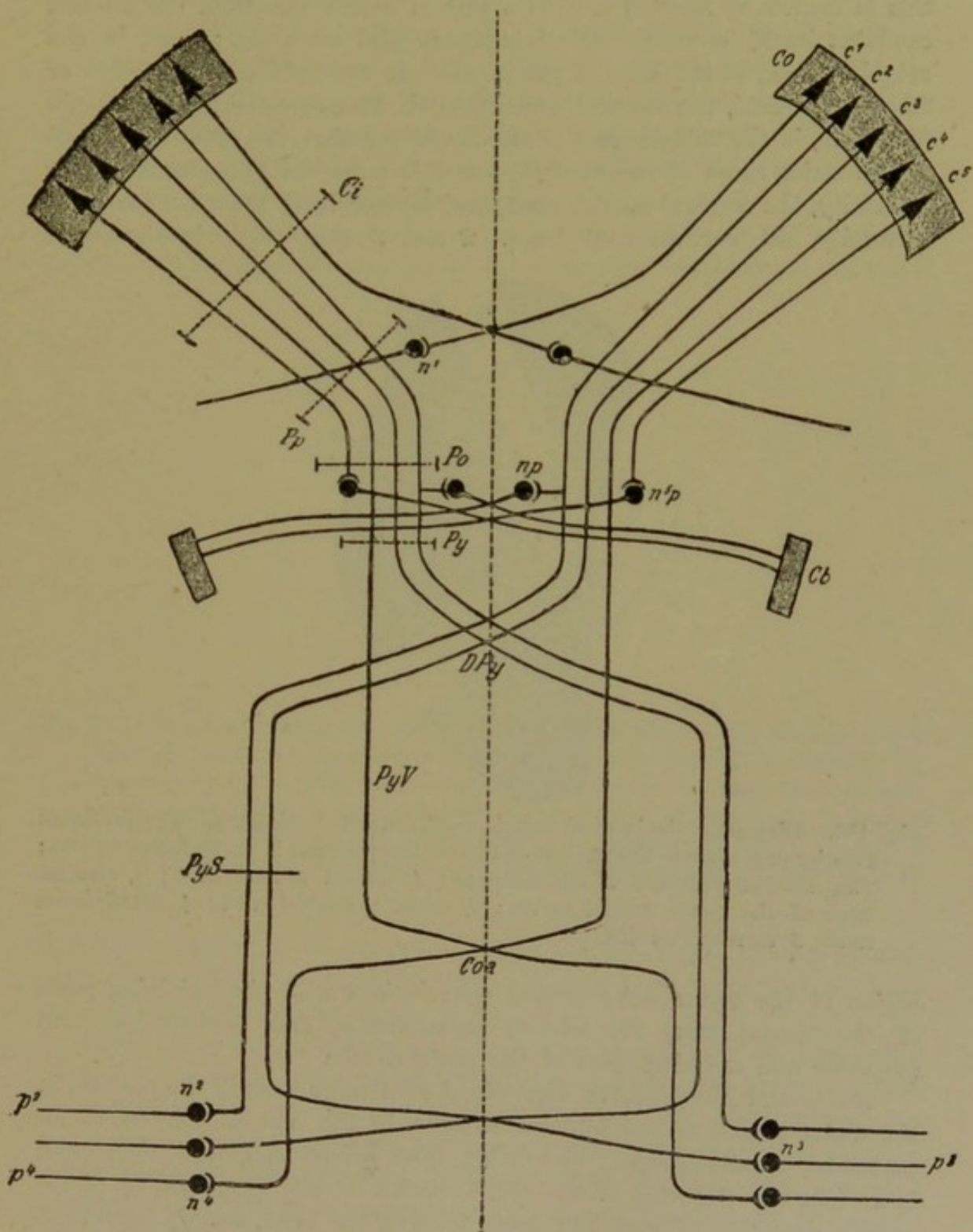


Fig. 155.—Scheme of pyramidal tracts.—Co, Cortex cerebri;  $c^1$  to  $c^5$ , pyramidal cells; Ci, internal capsule; Pp, crusta; Po, pons; Py, pyramids; Dl'y, decussation of the pyramids; PyV, anterior pyramidal tract; PyS, lateral pyramidal tract; Coa, anterior commissure; Cb, cerebellum; n, nucleus of a cranial nerve; p, peripheral end of the same; np and n'p, nuclei pontis;  $n^2$ ,  $n^3$ ,  $n^4$ , cells of the anterior horn;  $p^2$ ,  $p^3$ ,  $p^4$ , peripheral motor spinal nerves.



inner capsule. The whole anterior half of the anterior segment is occupied by a fibre-tract which we shall learn to know as the anterior peduncle of the thalamus (*Tho*). Behind this comes a tract of fibres, the frontal pontine tract (*1*), which streams in from the frontal lobe (though this is denied by *Zacher*) and to a certain extent also from the nucleus caudatus itself, in which last it probably also takes rise; next, in the neighbourhood of the knee of the capsule lie the cortico-bulbar tracts or faisceau geniculé, the cerebral connection of the motor nerves of the brain (*2*); then, in the anterior part of the hinder segment, the pyramidal tracts in the strict sense of the word (*3*)—first in order the fibres for the upper extremity, the cortico-brachial tract, and farther back those for the lower extremity, the cortico-crural tract. *2* and *3* take origin in the motor

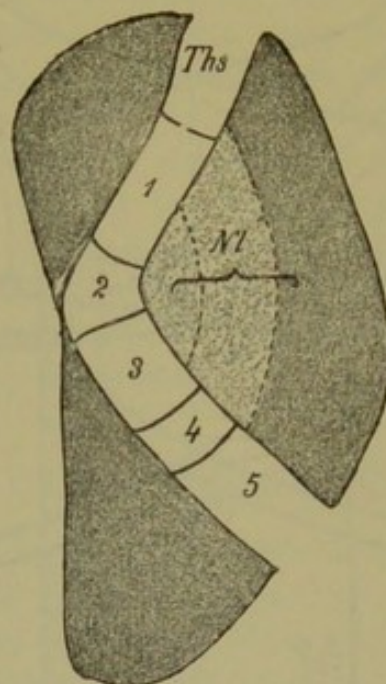


Fig. 156.—Diagram of the internal capsule.—*NL*, Nucleus lenticularis. The unmarked anterior grey mass is the nucleus caudatus, the posterior is the thalamus opticus; *Ths*, anterior peduncle of the thalamus; *1*, frontal pontine tract; *2*, cerebral tract of the motor cranial nerves; *3*, actual pyramidal tract; *4*, muscle-sense tract; *5*, carrefour sensitif.

region of the cortex—the central convolutions with the adjoining parts of the frontal lobe, the lobulus paracentralis, and, perhaps, a small (superior and anterior) part of the parietal lobe.

*Beevor* and *Horsley* have determined even more exactly the position in the motor region of the internal capsule in the apex of the tracts for particular muscle-groups. Proceeding from before backwards, their order is as follows:—Opening of the eye, deviation of the eyes, opening of the mouth, deviation of eyes and head, turning the head, tongue, corners of the mouth, shoulder, elbow, wrist, fingers, thumb, trunk, hip, ankle, knee, great toe, remaining toes.

Continuous with the posterior end of the motor pyramidal region of the internal capsule lies the field through which the centripetal tracts for muscle-sense course, the anterior being concerned with the upper



extremity, the posterior with the lower (*Redlich*). We do not know as yet in what part of the cortex they end (perhaps in the parietal lobe or the thalamus).

The posterior third of the hinder segment is devoted to the conduction of centripetal impressions (5). Some of the fibres rise in the pons and finally turn towards the temporal lobe (temporal pontine tract); while the hindmost fibres of the capsule turn backwards to the hinder part of the parietal lobe, to the occipital lobe (optic radiations, sagittal medullary layer of the occipital lobe), and also ventrally to the temporal lobes. Since various sensory tracts meet together in this region of the internal capsule it has been termed the 'carrefour sensitif.'

Other tracts which are present in the internal capsule will be mentioned later on. *Flechsig* calls attention to the important fact that the individual

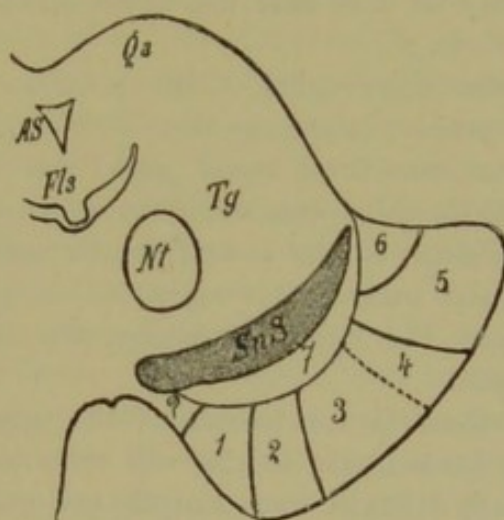


Fig. 157.—Diagram showing the constitution of the crus cerebri.—*Qa*, Anterior corpus quadrigeminum; *AS*, aquæductus Sylvii; *Fls*, posterior longitudinal bundle; *Tg*, tegment; *Nt*, red nucleus of the tegment; *SnS*, substantia nigra Soemmeringi; ? most mesial region, of uncertain meaning: 1, frontal pontine tract; 2, tract of motor cranial nerves; 3, pyramidal tract; 4, muscle-sense tract; 5, sensory portion of the crura; 6, fasciculus from the fillet to the crura; 7, stratum intermedium.

fibre-tracts traversing the internal capsule are inconstant in their relation to its knee; field 2, for example, does not always correspond to the knee itself, as represented in fig. 156.

These tracts from the internal capsule reach the base of the brain after passing between the grey masses of the 'tween-brain and fore-brain, and there constitute the pes pedunculi or crura, *Pp*. We can picture to ourselves the displacement which the fibres undergo, by imagining that the whole crura is slightly twisted, its hindmost fibres (5), to which we have ascribed sensory functions, appearing in horizontal section on the lateral side of the crura, its anterior fibres (1) on the mesial side, and the intermediate bundles (2, 3, 4) maintaining the same sequence as before.

Thus in the crescent-shaped cross-section of the crura, proceeding from within outwards, we find:—

1. The frontal pontine tract (1). After disease of the frontal lobe or



the anterior part of the inner capsule, this tract degenerates as far as the pons, but not farther, and ends in the ventral cell-group there (fig. 155,  $c^5$ — $n^5p$ ). Generally, however, a thin tract of fibres on the inner border of the crus is exempt from degeneration. To this we must allow a different course, unknown as yet.

2. Next comes the cortico-bulbar tract (2), connecting the cortex with the motor nerves (trigeminus, abducens, facialis, glossopharyngeus, vagus, hypoglossus) which take origin in the region of the medulla oblongata. It is very probable that all these fibres turn first mesially and then dorsally in or immediately below the region of the pons, cross in the raphe, and finally reach the motor nuclei of the nerves in question, to influence the cells of origin by means of their arborescent processes, either directly or through intercalary cells. Similar conditions must exist for the nucleus nervi oculomotorii, only in that case the fibres must have left the tract higher up (fig. 155,  $c^1$ ,  $n^1$ ,  $p^1$ ).

3. Next in order comes the region of the spinal cortico-muscular tracts, the pyramidal tract proper (starting from  $c^2$ ,  $c^3$ ,  $c^4$ ). If we divide the cross-section of the crus into three equal parts, this tract would roughly correspond to the middle third (according to *Charcot* to its two middle fourths, according to *Zacher* to the second fourth only, counting from the lateral side). The mesial part of this region (3) is probably occupied by the tracts which supply the upper extremity, the lateral part by those which supply the lower.

The circumstance that the movements of the upper extremity are not only more completely subordinate to the will than those of the lower but are also far more varied, delicate, and complicated, gives a certain value to the supposition of *Onanoff* and *Blocq* that five times as many pyramidal fibres are destined for the former as for the latter.

Owing to the far from parallel course of the fibres in the crusta (they tend to converge inwards in their course spinewards), it may easily happen that many degenerated bundles remain hidden in its depth, so that only a triangular grey-coloured area shows from the surface in certain cases of descending degeneration of the pyramidal tracts; the apex of the triangle points towards the pons, its base is covered by the optic tract.

4. Laterally from the pyramidal tracts we may expect to find the conducting paths of muscle-sensibility (4).

5. The lateral bundles of the crusta (5) can be followed brainwards into the sensory region of the internal capsule. Most likely they all, or at least the majority of them, take rise at the level of the pons. Usually they are spared in secondary descending degeneration; in exceptional cases, however, as *Kreuser* has observed, they are drawn into an extensive descending degeneration, a circumstance which may be regarded as opposed to their sensory interpretation.

The denotation of these tracts as Turck's bundle, sometimes adopted, should be avoided, since the name is usually applied to the anterior pyramidal tract.



This temporal pontine tract is supposed to extend to the dorsal nerve-cell groups of the pons (*Jelgersma*), while the frontal pontine tract, as already mentioned, ends in the ganglia of the pons seen in cross-section on the ventral side of the pyramids.

6. In the most cerebral part of the crusta we find, in its lateral angle, another bundle (6), which curls around the outer side of the crus downwards and inwards, so that it has reached its mesial border by the time it arrives at the upper edge of the pons. It then turns dorsalwards and passes into the region of the fillet, and becomes thenceforward the mesial portion of the mesial fillet (bundle from the crus, mesial pontine bundle of the fillet, *faisceau en écharpe*). It remains intact when other parts of the crus degenerate downwards, and can then be distinguished from the grey degenerated columns on which it lies as a conspicuous white band. In many animals this bundle attains to a very striking development relatively to the slender crus. Its brainward course is not known.

7. Between these parts of the crusta and the substantia nigra Soemmeringi (*SnS*), which lies to its dorsal side, we observe in the cross-section a crescent-shaped tract of fine fibres, the stratum intermedium (7). A connection certainly exists between these fibres and the cells of the substantia nigra. They are said to come down from the basal ganglia.

Following the crusta downwards, we see that all the fibres which compose it enter the pons (fig. 155, *Po*) and that the bundle which appears as its continuation on the ventral side of the pons (the pyramid, *Py*) is greatly diminished in size. This is because the fibres classed under 1, 2, and 3 have been lost in the pons in the manner described. We cannot tell with certainty whether any of the fibres belonging to the pyramidal region proper end in the pons.

If a cross-section through the pons be examined, numerous clumps of grey substance very rich in small cells are seen lying among the cross-cut bundles which are descending from the brain to the medulla, as well as among the fibres from the cerebellum to the pons, which are here cut lengthways. These cells (fig. 155, *np* and *n<sup>b</sup>p*) send out very fine nerve-fibres which turn ventralwards, usually with an inclination inwards, and, after crossing the middle line, constitute the contra-lateral brachium pontis and enter the cerebellum (*Cb*). A small number of them are lost in the brachium pontis of the same side (*Ramón y Cajal*). Since the pyramidal fibres are supposed to give off numerous collaterals within the pons, which break up among the neighbouring cell-groups, a close connection is thus provided between the cerebrum and the contra-lateral hemisphere of the cerebellum. Other fibres of the pons, distinguished by their larger calibre and earlier acquisition of the myelin-sheath, seem to take origin in Purkinje's cells of the cerebellum. They are found chiefly in the deeper (dorsal) parts of the pons, cross the middle line there, and turn dorsalwards in the region of the tegment. Opinions differ as to the fate of these fibres. Some of them are prolonged into the raphe tegmenti, and, according to *Bechterew*, find their destination for the present in the groups of nerve-cells which lie on either side of the raphe (nucleus reticu-



laris tegmenti pontis), *Nrtg*, fig. 141. According to *Ramón y Cajal*, most of them divide in the lateral part of the tegment into an ascending and a descending branch, of which the former is the thicker.

It has already been mentioned that the frontal and temporal pontine tracts end (or, it may be, originate) in the cell-groups of the pons. *Van Gehuchten* is of opinion that descending fibres of two kinds originate from the motor region of the cortex, one descending to the cord (cortico-spinal fibres), the other ending in the nuclei of the pons (cortico-cerebellar fibres).

The pyramids, which we see pass downwards from the ventral side of the pons in the form of compact columns (the diameter of that on the left invariably exceeding that of the right by from 11 to 14 mm., according to *Gattel*), quickly diminish in cross-section as they sink into the medullary substance, and disappear from the surface completely at the lower end of the medulla oblongata.

This disappearance is largely due to the fact that in the depth of the medulla, before reaching the central canal, most of the fibres of the pyramids cross the middle line (decussatio pyramidum) and enter the lateral column on the opposite side.

The crossing of the lateral tracts extends to the level of the second cervical nerves, **decussatio pyramidum, DP**. Histologically, it is characterised by the fact that the fibres which, descending backwards and medianwards, cross one another in this decussation, do not cross as isolated fibres but in bundles; this gives rise to a peculiar appearance in cross-section (figs. 132, 133), something like what is known as herring-bone pattern.

It is, however, unusual for all the fibres of the pyramids to enter this decussation and so constitute the lateral pyramidal tract (*PyS*) of the opposite side. A portion of the tract does not cross, but runs directly caudalwards in the anterior column (*PyV*) of the same side.

The relative size of the crossed and uncrossed portions of the pyramidal tracts within the spinal cord and at the decussation is subject to numerous individual differences. *Flechsig* has made it the subject of detailed communications. Both anterior and lateral tracts are found in the majority of spinal cords (75 per cent.); the lateral is so much the larger, however, that beneath the decussation it usually gets from 91 to 97 per cent. of all the pyramidal fibres, while the anterior tract only gets from 3 to 9 per cent. Nevertheless, this relation is exceedingly variable; it may happen that all the pyramidal fibres cross (total decussation in 11 per cent. of all spinal cords), in which case no anterior tract comes into existence; on the other hand, this total crossing may only affect the pyramidal fibres of one side. Further, it may happen that nine-tenths of the fibres of the pyramid remain on the same side in the anterior tract, and only one-tenth passes across the middle line to the opposite lateral tract. In the latter case, the opposite lateral pyramidal tract appears abnormally small, while the anterior tract of the same side is conspicuous for its great size. A



symmetrical disposition of the two tracts on each side occurs in only 60 per cent. of all cases; in the remaining 40 per cent. the one pyramid is not split into anterior (direct) and lateral (crossed) tracts in the same proportion as the other.

In descending degeneration after unilateral lesions of the brain we almost always observe a more or less noticeable loss of fibres in the lateral pyramidal tract of the same side (fig. 122), and we are therefore justified in assuming that a varying, though usually small, proportion of the pyramidal fibres enter the lateral pyramidal column without crossing. This view is, in fact, capable of direct demonstration in preparations of degenerated tissue.

The lateral pyramidal tract decreases constantly in cross-section downwards to the caudal end of the cord, the reduction proceeding most rapidly in the swellings. The reason of this is that the fibres turn successively in a mesial direction and enter the grey substance of the anterior horn ( $n^2$ ,  $n^3$ ,  $n^4$ ), where they break up into arborescent systems. It has, indeed, generally been taken for granted that they there joined the motor cells of the anterior horn directly, but the recent supposition of *Monakow* that Golgi's cells are intercalated between the ends of the pyramidal fibres and the cells of the anterior horn seems not without foundation. Even in successful *Marchi's* preparations, which would be best adapted for the purpose, no pyramidal fibres can be seen to bend round directly into the anterior horn.

We have also learnt that single fibres of the lateral pyramidal tract cross the middle line in the anterior commissure, and thus arrive at the mesial cell-group ( $n^3$ ) of the contra-lateral anterior horn.

The anterior pyramidal tract can hardly ever be followed as far as the upper dorsal cord. The most probable theory seems to be that its fibres pass by degrees, by way of the anterior commissure, *Coa*, and through the grey substance, into the lateral pyramidal column of the opposite side. The possibility that some of them enter into direct relations with the cells of the anterior horn on either side must be taken into account.

From the cells of the anterior horn we see the fibres of the anterior spinal roots issue ( $p^2$ ,  $p^3$ ,  $p^4$ ), the great majority of them being destined for voluntary muscles. Thus it is seen that the pyramidal tract is a long unbroken fibre-route between the cells of the cortex of the great brain (especially that part of it to which we attribute motor functions) and the cells of origin of the motor nerves. For the larger part this connection is a crossed one; some fibres, however, run without crossing. The cortico-muscular tract consists, therefore, of two sets of constituents or neurons: (1) cells of the cortex with the pyramidal fibres which rise from them; and (2) cells of the anterior horn (and the corresponding cells of the nuclei of the cerebral nerves), with the peripheral motor fibres which extend to the muscles.

The pyramidal fibres, however, are supposed to give off collaterals on their way from the cortex to the motor cells of the cord, more



especially during their passage through the pons. It has already been mentioned that these collaterals, by joining on to the cells of the ganglia of the pons, form the connecting link with the contra-lateral hemisphere of the cerebellum. In the spinal cord also, at least in the embryo, the pyramidal fibres are rich in collaterals.

Wherever the pyramidal tract is injured, either in its course or in the cerebral region into which it extends, the lesion forms the starting-point of descending degeneration. This advances uninterruptedly down the cord, but stops short of the cells of the anterior horn. But even after spinal lesions the cross-section shows a considerable number of sound fibres in the degenerated area. These perhaps represent a system independent of the pyramids.

Certain differences which fall under observation in the areas which degenerate after cerebral and spinal lesions have already been pointed out.

*Meynert* has called attention to the fact that in Man, as in all other mammals, the cross-section of the crura greatly exceeds in extent that of the tegment, a fact of great importance which must be mentioned in this place, since the pyramidal tracts constitute a considerable portion of the crura. *Spitzka* has found that not only has the dolphin, which is destitute of hind limbs, rudimentary pyramids, but the same condition obtains also in the elephant and armadillo. On the other hand, in the seal, which is also provided with the mere rudiments of extremities, the pyramids are relatively larger than in the dog, although the brains of the two animals appear to be closely related in internal structure (*Hatschek*).

The higher the animal stands in the scale the greater is the part played by the pyramids in the performance of voluntary movements, as would, indeed, be expected from these details of structure. But, as the experiments of *Wagner* and *Starlinger* convincingly demonstrate, they are by no means the only motor tracts which convey impulses from the cortex to the muscle-system, since after complete severance of the pyramids in the dog its movements are hardly to be distinguished from those of the uninjured animal.

It has already been pointed out (p. 236) that in many animals the pyramidal tracts run either entirely or in part in the posterior columns.

Again, attention must be called to the fact that the pyramidal tracts first become medullated in the centrum semiovale, and that the myelination proceeds from above downwards, taking several weeks to reach the lumbar cord.

**2. The Posterior Columns and the Tracts derived from them.**—A great part of the fibres of the posterior columns stand in direct relation with the posterior roots. The bulk of the fibres here met with must be looked upon as the intramedullary continuation of the posterior root-fibres which rise in the cells of the spinal ganglia; not of those only which ascend directly to the brain (or, in some cases, descend caudalwards), but also of their collaterals. To certain regions of



the cross-section, such as the ventral posterior column-field, Schultze's comma, and the dorso-mesial sacral bundle, a different meaning, as we have seen, must be ascribed.

In the medulla oblongata, as we know, the posterior columns swell out, owing to the deposition in them of certain grey masses (nuclei funiculi gracilis et cuneati), *Nc*, *Ng* (fig. 158). The cells of these grey masses come into relation with the arborescent processes of the ascending fibres of the posterior columns. Both nuclei, considered together, may be termed shortly the nuclei of the posterior columns. The grey substance of the nucleus funiculi gracilis forms a fairly uniform continuous mass; that of the nucleus funiculi cuneati is divided into distinct and irregular groups, containing both large and small cells. The larger are found chiefly in the lateral groups (nucleus funiculi cuneati exterior) and extend farther brainwards than the groups of small cells. They must, according to the data already given, be looked upon as sensory nuclei for the muscle-sense of the extremities. Burdach's nucleus is supposed to be in relation with the upper limb; Goll's nucleus with the lower limb.

The fibres coming out of these nuclei, the indirect connections of the posterior columns, that is to say, go partly to the corpora quadrigemina and the great brain *viâ* the fillet; partly to the cerebellum *viâ* its inferior peduncle, the corpus restiforme. We must, therefore, leaving out of account some less well-known connections, consider these two separately.

(a.) **The Fillet.**—The term fillet (lemniscus, laqueus, ruban de Reil) was originally applied to the triangular area on the surface of the crus, which extends downwards and backwards from the posterior tubercle of the corpora quadrigemina. Latterly the term fillet has been made to include also other allied fibre-tracts. This composite system has been divided in several ways without anything like uniformity in nomenclature. The difficulties which beset the subject are due as much to a confusion of names as to a complexity of structure. We will here distinguish two main divisions, the mesial (or superior) and the lateral (or inferior) fillet. We are still, however, far from understanding the origin and destination of all its fibres. The part of the fillet best established is that which is in indirect connection with the posterior columns of the spinal cord; this is our reason for considering it here.

First we will turn our attention to the mesial fillet (*Lmm*), which extends much further down than the other.

We have seen that arcuate fibres extend from the nuclei of the posterior columns, and probably also from the substantia gelatinosa of the fifth and ninth cranial roots, ventrally towards the middle line. Many of these fibres, especially those which are found at the spinal end of the medulla oblongata (fig. 134), arch round the central canal in a bold curve and take up their position after crossing (decussation of the fillets, *DLM*) on the dorsal side of the pyramids in the inter-olivary region or 'fillet layer' (fig. 134 *et seq.*, *Lm*). Further, it is probable that a small



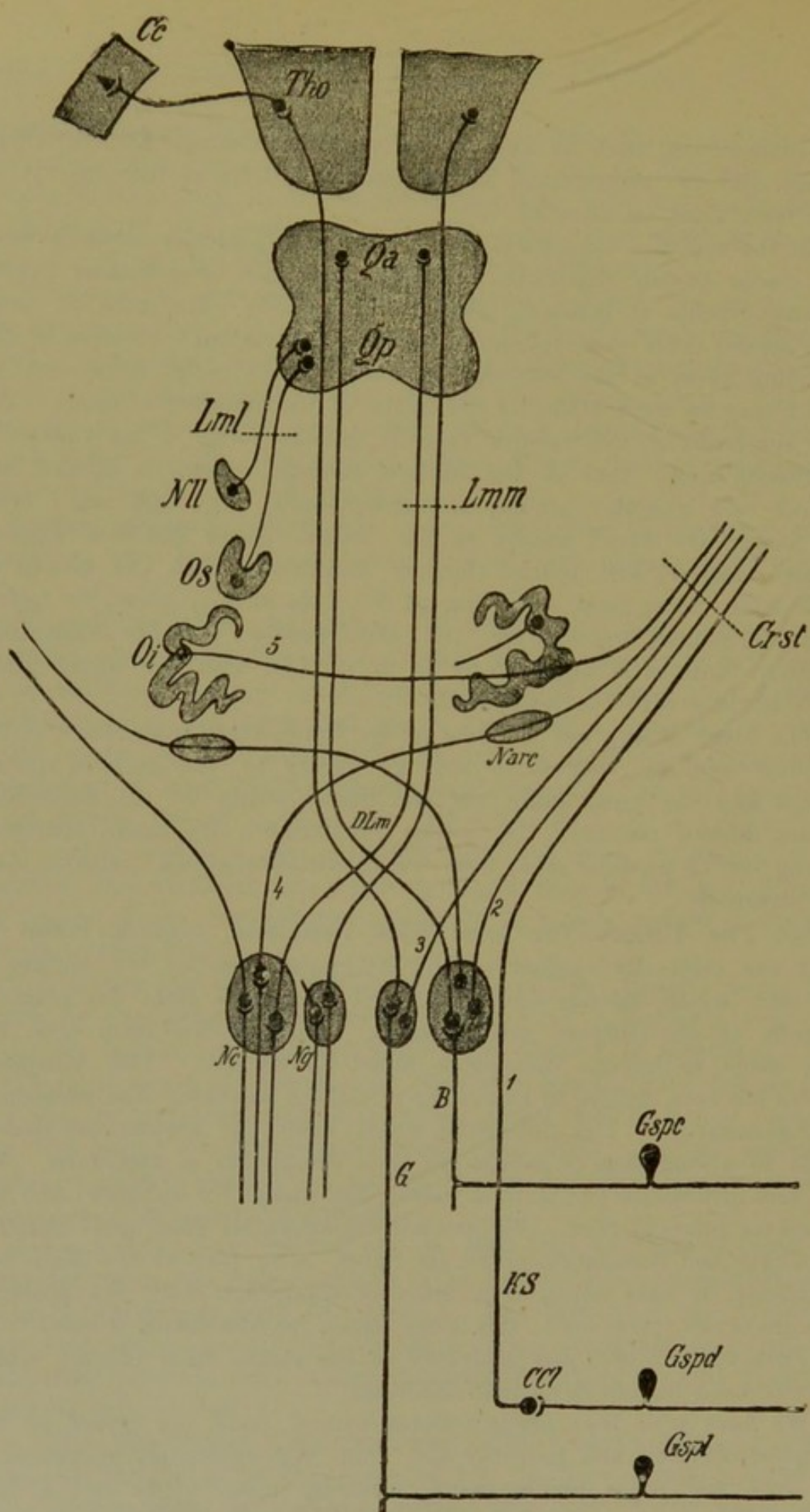


Fig. 158.—Plan of the central connections of the posterior columns.—*Gsp*, Ganglion spinale (*l*, lumbalis; *d*, dorsalis; *c*, cervicalis); *CCL*, Clarke's columns; *KS*, lateral cerebellar tract; *G*, Goll's column; *B*, Burdach's column; *Ng*, nucleus gracilis; *Nc*, nucleus cuneatus; *DLm*, decussatio lemnisci; *Crst*, corpus restiforme; *Narc*, nucleus arcuatus; *Oi*, inferior olive; *Os*, superior olive; *Lmm*, mesial fillet; *Lml*, lateral fillet; *Nll*, nucleus of lateral fillet; *Qp*, *Qa*, posterior and anterior corpora quadrigemina; *Tho*, thalamus opticus; *Cc*, cortex cerebri.



proportion of them do not enter the decussation, but pass into the fillet on the same side. The fibres of the fillet may, perhaps, be joined by fibres from the anterior column. *Edinger* regards this accession as the central sensory tract of the spinal nerves, composed of fibres which take origin in the posterior horn, cross in the anterior commissure, and so reach the anterior column.

In sections nearer the brain (figs. 135, 136) we see the fibræ arcuatæ internæ (*fai*) sweeping down in finer bundles, and some of them in wider curves. Some are collected into the mesial region of the medulla oblongata (near the substantia reticularis alba) to the dorsal side of the proper inter-olivary layer, and there bend round brainwards; others keep the horizontal direction, and, as we shall presently see, join the corpus restiforme on the opposite side. The fibræ arcuatæ which take origin in the cells of Burdach's column are the first to be myelinated (in the seventh month of embryonic life); the fibres from Goll's columns do not acquire the myelin sheath till the ninth month (*Edinger*, though *Bechterew* places it earlier).

The cross-section of the mesial fillet lying in the ventral part of the tegment, where it is pierced by fibres of the corpus trapezoides, *Tr* (fig. 139 *et seq.*), can be followed into the mid-brain as a transversely placed oval field lying on the dorsal side of the pons (figs. 154 and 158, *Lm*). The lateral half of this area is supposed to originate from the nucleus cuneatus, the mesial half from the nucleus gracilis. One can recognise a steady increase in the size of this field, which enlargement must be attributed to the accession of new fibres of doubtful origin. Possibly the fibres of the pons which ascend through the raphe to the fillet may bring an accession from the cerebellum. It is a more important circumstance, however, that most sensory nuclei have crossed connections with the fillet, and this, even apart from its origin in the posterior columns, would mark it as a sensory tract. Near the middle of the cross-section of the fillet little clumps of nerve-cells occur (called by *Roller* the 'fillet-nuclei,' nuclei lemnisci mediales), which may be regarded as the centres of origin of fillet-fibres. *Bechterew* finds a double accession of fibres from his nucleus reticularis tegmenti pontis, *Nrtg* (fig. 141). From the crusta, too, fibres are said to ascend and mingle with the fillet (the scattered fasciculi of the fillet). These are not medullated at birth.

Among the fibres of the fillet we observe (especially at the level of the corpora quadrigemina) many large bundles of finer fibres; whence it is clear that fibres of different kinds take their separate course through the region of the mesial fillet. We may, therefore, take for granted that numerous short tracts run uncrossed throughout the region of the fillet. Another uncrossed portion of the fillet consists of a bundle which originates in part in the medulla oblongata (fillet of the crusta, mesial pontine bundle of the fillet). Farther up it lies on the mesial border of the fillet, and turns ventralwards in the vicinity of the anterior margin of the pons. This bundle passes round the crus cerebri in the manner described on p. 284. Under the name of the lateral pontine bundle



*Schlesinger* describes fibres which first come into view in the uppermost planes of the medulla oblongata, and increase in size rapidly in the vicinity of the pons, where they occupy the ventral portion of the fillet in the middle third of its breadth. These fibres (lemniscus accessorius of *Bechterew*) also pass into the crusta in the uppermost planes of the pons. *Schlesinger* thinks that in the last-named bundle we have the cerebral connections of the sensory nerves, while *Hoche* prefers to suppose that they contain the central connections of the facial and hypoglossal nerves.

At the level of the exit of the trigeminus, and directly its end nuclei have disappeared, another part of the fillet becomes conspicuous at the side of the section, the lateral fillet, *Lml*. Since the parts of the mesial fillet which lie nearest the middle line now become increasingly distinct from the rest, the section is naturally disposed in three divisions (fig. 146):—(1) The most mesial bundle, called the bundle from the fillet to the crusta, *LmP*; (2) the mesial fillet, *Lmm*; (3) the lateral fillet, *Lml*. The nucleus of the lateral fillet (nucleus lemnisci lateralis, fig. 144, *Nlml*, and fig. 158, *Nll*) yields numerous fibres to the lateral fillet, as does also the upper olive, *Os*. It receives, too, a considerable addition from the corpus trapezoides and the striæ medullares nervi acustici on the other side (*Monakow*). The lateral-fillet-nucleus corresponds in position to the upper olive, the cerebral end of which it almost reaches. To this is added the accession from the nucleus reticularis before mentioned. The lateral fillet, which, as it covers the brachium, is the part visible on the exterior, extends to the corpora quadrigemina post. (*Qp*), and crosses in part above the aqueduct. A portion of it even extends to the anterior corpora quadrigemina. *Feld* found fibres which, starting from the lateral fillet, pass on the ventral side of the posterior longitudinal bundle to the contra-lateral posterior corpora quadrigemina. Thus a double crossed connection exists between the lateral fillet and the corpora quadrigemina. The lateral fillet is also called the inferior fillet, while the mesial fillet, a great part of which can be followed cerebralwards as far as the great brain, is also known as the superior fillet.

Fibres from the lateral column of the cord also enter the nucleus reticularis, and we may consider that thus a connection is established between the lateral column and the posterior corpus quadrigeminum.

Another connection, between this last and the lateral column on the same side, is formed by a bundle of fibres which can be followed caudalwards from the lateral nucleus of the fillet. Passing to the lateral side of the nucleus facialis, and on between the upper olive and the spinal root of the trigeminus, it forms a not very compact bundle in the middle of the lateral column (lateral fillet tract of *Ferrier* and *Turner*).

The most mesial bundle of the mesial fillet becomes distinctly separate from the rest in the region of the corpora quadrigemina, and turns at once ventralwards to the crusta, following the proximal border of the pons (*cf.* fig. 148). Hence it is sometimes called the bundle of the crusta, or mesial accessory bundle of the fillet.



The principal part of the upper or mesial fillet turns dorsally under the anterior corpus quadrigeminum to form its white matter, just in the same way as the lateral fillet has been seen to do with regard to the posterior tubercle. Possibly a part of the fibres lying above the aqueduct are continued across the middle line to the tubercles of the opposite side, but whether or not they extend into the brachia corporum quadrigemorum is uncertain. A considerable remnant of the fillet is to be traced still farther brainwards, on the outer side and a little dorsally to the red nucleus, as a feebly marked half-moon-shaped bundle (fig. 149, *Lm*), mixed with the fibres which stream out from the nuclei of the regio subthalamica. These fibres, or at least the greater number of them, end in the ventral part of the thalamus, *Tho* (inclusive, according to *Déjerine*, of the centre médian).

*Flechsig* and *Hösel* have stated that a very considerable part of the fillet streams directly into the cortex, but the results obtained by all later observers (*Mahaim*, *Déjerine*, *Bikeles*, *Bielschowsky*, *Monakow*, and others) oblige us to conclude that the fibres which do so form a very insignificant part of the mesial fillet, and that the ventral and lateral parts of the optic thalamus must be regarded as the main terminus for such part of it as passes beyond the corpora quadrigemina. There are, indeed, fibres which start from cells in this region and stream into the cortex, *Cc* (parietal lobe?). We can therefore speak of a fillet of the cortex in the sense that impulses conducted centripetally through certain fibres of the mesial fillet do finally reach the cortex by way of the cells of the thalamus.

Secondary degeneration of the fillet never occurs as a consequence of lesion of the cortex of the brain. Only, when the injury is of very long standing, a simple atrophy or attenuation of single fibres may be observed. This seems to prove that the tract connecting the cortex and fillet must consist of several neurons. The same result has been produced by experiments upon young animals.

If the fillet itself is injured, both ascending and descending degeneration may be observed. Formerly the latter was supposed to be the rule. Of course, when the seat of the injury is at the point where the fillet streams into the thalamus, only descending degeneration must be looked for. It will not, however, be very extensive at the lower levels; certainly less so than if the injury were nearer the cord, say, in the region of the pons. In the former case the part of the fillet which ends before reaching the thalamus, in the corpora quadrigemina, for instance, is unaffected. *Déjerine* explains this circumstance on the assumption that here we have to do with cellipetal degeneration, which is more complete according to the propinquity of the lesion to the cells of origin, especially if the latter lie in the posterior columns.

When, however, the mesial fillet is injured in its course, it comes to grief principally in the upward direction, which is properly the direction of cellifugal degeneration. The same thing happens if the lesion affects the inter-olivary layer, or the arcuate fibres from the nuclei of the posterior



column (as in syringo-myelia), or the nuclei themselves. This degeneration can never be followed beyond the thalamus opticus.

It is certain that in the mesial fillet we have one of the most important of the sensory tracts, perhaps the principal conducting-path of muscle-sensibility. With regard to the conducting-paths for skin-sensibility, we have so far no adequate grounds on which to base any conclusion.

Neither can we say positively whether any descending fibres (taking origin, perhaps, in the cells of the thalamus) run their course in the fillet.

The lateral fillet stands in intimate relation to the sense of hearing, and will, therefore, be more fully described in connection with the auditory nerve.

(b.) **The Inferior Peduncle of the Cerebellum.**—The connection of the posterior column with the cerebellum is effected by a part of the peduncle of the latter (corpus restiforme or inferior peduncle). The passage over from the posterior column to the peduncle of the cerebellum is not, however, so simple as a superficial examination of the medulla would lead one to suppose.

Into the constitution of the cerebellar peduncle enter—(1) fibres which conduct impulses upwards from the spinal cord, both from its lateral column and from its posterior column; (2) fibres from the inferior olivary nucleus (olivary cerebellar tract).

### 1. Its Spinal Constituents.

(a.) The fibres derived from the lateral column constitute the lateral cerebellar tract, *KS* (fig. 158, 1), which we will again mention later on. The fibres which compose it are early invested with the myelin sheath, and are conspicuous even at birth by their colour when treated by methods of medullary-sheath staining. They then form the central region of the cross-section of the cerebellar peduncle. It is supposed that the restiform body receives a further accession of fibres from the nucleus of the lateral column which lies fairly near to the lateral cerebellar tract (figs. 135–137, *Nlt*).

(b.) The constituent of the restiform body derived from the posterior column is a very considerable one; partly direct, partly crossed; *Darkschewitsch* and *Freud* have again pointed out the importance of the uncrossed connection, which had for a long time been overlooked. They have shown that the corpus restiforme receives a much more considerable accession of fibres from the nuclei of the posterior column of the same side, especially from Burdach's nucleus (fig. 158, *Crst*, 2, 3), than it does from the arcuate fibres; the latter extend a short distance on the posterior aspect of the periphery of the medulla, and connect the restiform body with Goll's nucleus (*fibræ arcuatæ externæ posteriores*). At the higher levels of the nuclei of the posterior columns, it can be shown that they decrease as fast as the corpus restiforme grows; the latter occupies the place of the successively disappearing clumps of grey matter (*cf.* figs. 136, 137, 138). In the nucleus cuneatus, only the large cells



are supposed to give origin to fibres which proceed to the corpus restiforme.

The restiform body receives a further reinforcement of fibres from the posterior column by a round-about way through the *fibrae arcuatae internae* (figs. 135, 136, *Fai*), which constitute, as has already been briefly explained (p. 309), the proximal continuation of the crossed fillet. Collected in slender bundles, they traverse in graceful curves nearly the whole interval between the pyramids and the nerve-nuclei on the floor of the fourth ventricle. Not a few of them pass through the olivary nucleus (fig. 139), but, apparently, without forming connections with it. In this way they reach the raphe, and immediately turn ventralwards, cross, and pass downwards on either side of it, often in massive bundles. The mesial periphery of the contra-lateral pyramid reached, they sweep onwards over the surface of the pyramid of the opposite side and over the olive to the corpus restiforme. These are the *fibrae arcuatae externae anteriores* (fig. 158, 4). Thus they connect the posterior column with the corpus restiforme of the opposite side. Certain small collections of grey matter, as well as the larger nucleus pyramidalis anterior (nucleus arciformis), are imbedded in the course of these fibres (fig. 135 and the following figs., *Narc*; fig. 158, *Nar*). The largest cells lie in the centre of the nucleus (*Mingazzini*). It is certain that some *fibrae arcuatae* end and others originate in the anterior pyramidal nuclei, which are precursors of the nuclei of the pons. Between them and the olivary nucleus, round which they take their subsequent course, there is everywhere interposed a layer of fibres (the 'fleece' or *stratum zonale olivae*) which forms its immediate envelope.

A tolerably large proportion of the *fibrae arcuatae externae* take origin in the nuclei of the lateral column. These fibres are said to form the dorsal boundary of the nucleus arcuatus (*stratum dorsale* of *Mingazzini*) and to be principally connected with its superior or cerebral half.

## 2. Olivary Constituent.

(c.) The olivary portion of the corpus restiforme is also constituted in a complicated way.

The **olivary nucleus** (inferior olive, figs. 135, 139, and 154) appears on cross-section as a double sinuous plicated band, of which the two segments are united laterally, but are open towards the middle line. As a whole, the inferior olive may most readily be compared to a bag, the mouth of which is only partly drawn together, the hole into it (*hilum*) being directed medianwards. The thickness of the band is almost uniform throughout, between 0.3 and 0.4 mm. With slight magnification one can see that numerous nerve-bundles, some of them very considerable, like the hypoglossal root, traverse the substance of the olive. The nerve-cells of the olive are round or somewhat fusiform, slightly pigmented, and almost all of the same size (12 to 20  $\mu$  in diameter). They are fairly evenly distributed throughout the grey band, although occasionally some cells lie



outside the grey substance. Besides the bundles of fibres which pierce the grey band in a horizontal or longitudinal direction, a rich network of medullated nerve can be shown to exist within the grey substance of the olive. The silver-method of impregnation exhibits the characteristic shape of the cells of the olivary nucleus. Especially striking is the abundance of dendrites, which branch out into a peculiarly rich tangled network. The axis-cylinder processes start in every conceivable direction, but for the most part end by turning towards the raphe, probably to reach the contra-lateral corpus restiforme. Some of these fibres are said, however, to pass into the corpus restiforme of the same side (*Ramón y Cajal*). Moreover, quantities of fibres, from within and from without, pass into the grey substance of the olive (Kölliker's internal fibres), and break up into very rich end-ramifications among its cells. The two accessory olives exhibit a similar structure.

In no animals do we find the plaitings of the olivary nuclei as delicate or abundant as in Man. The accessory olives exhibit, moreover, very different degrees of development in different animals. In the dolphin, for instance, the anterior accessory olives are represented by two massive rounded bodies, which might easily be mistaken for the pyramids.

Numerous groups of fibres come out of the hilum (they constitute the peduncle of the olive); others envelop its outer side, the individual fibres having a horizontal direction (stratum zonale). Lastly, a considerable number of fibres extend from the stratum zonale to the restiform body, passing by the outer border of the spinal root of the trigeminus (figs. 136, 137).

It is not possible by anatomical methods to distinguish between the several sets of fibres described above. We must be influenced in this matter by pathological observations, the most notable being that when one side of the cerebellum atrophies the opposite olive atrophies also.

It would seem that the course of the fibres connecting the olive with the corpus restiforme is as follows:—The fibres, which take origin in the olive, come out of the hilum and pass through and on the ventral side of the anterior accessory olive (which here consists only of a dorso-ventral part) towards the raphe. There they cross the middle line obliquely, piercing the contra-lateral olive for the most part, and also taking part in the formation of its stratum zonale (fig. 158, 5). These fibres, most of which are coarse, form undulating bundles on their way from the olive to the corpus restiforme of the same side; some of them running on the mesial side of the substantia gelatinosa, some through it and through the spinal root of the fifth nerve, and others, finally, on the lateral side of the fifth nerve to the periphery. All but the last-named belong, like the fibres of the fillet, to the *fibræ arcuatæ internæ*; but, while the fibres belonging to the fillet are myelinated in the seventh month of foetal life, those of the olive and the corpus restiforme do not acquire their sheaths till later. The only connection that has been proved in the case of the inferior olive is the crossed (and, to a much smaller extent, uncrossed)



connection with the cerebellum. Others must surely exist, but at present they are unknown.

*Kölliker* and *Held*, in opposition to most writers, hold that the fibres connecting the olive and cerebellum take origin in the Purkinje's cells of the latter and end in the former. They would thus represent a centrifugal portion of the corpus restiforme. According to *Kölliker*, the nerve-processes of the olivary cells become fibres which cross in the raphe, descend as longitudinal fibres into the lateral column, and finally reach the motor nuclei of the cord.

*Bechterew* and *Flechsig* have described a connection between the inferior olive and the nucleus lenticularis *viâ* the central tegmental tract. This bundle is gradually formed on the lateral and dorsal surface of the inferior olive, passes between the mesial fillet and the superior olive (figs. 140 and 141 *cH*), continues its course towards the cerebrum on the lateral side of the posterior longitudinal bundle, and, lastly, enters the ansa lenticularis and the posterior commissure (*Helweg*). The central tegmental tract is rarely distinctly marked in adult brains.

The inferior peduncle, formed by the union of all the tracts of fibres above described, soon enters the substance of the cerebellum (figs. 141, 143), in which its further course can only be followed by embryological methods.

According to *Edinger*, the spinal portion of the restiform body is destined for the vermis, whilst the olivary elements form the bundles of fibres which surround the corpus dentatum as its 'stratum zonale.' Further details will be mentioned in connection with the cerebellum. The tracts of fibres which pass from the fifth and eighth nerves into the cerebellum are also frequently reckoned to the corpus restiforme. Thus we see that the corpus restiforme contains (perhaps entirely consists of) numerous centripetal tracts which end in the cerebellum. We shall return to the question of its significance when we come to treat of the cerebellum.

**3. The Lateral Cerebellar Tract.**—The facts known with regard to this may be recapitulated here in a few words (fig. 158, 1). The lateral cerebellar tract receives its fibres from Clarke's column, where, as we know, posterior root-fibres terminate. Its conspicuously large fibres pass laterally to the periphery of the lateral column, and there turn brainwards. When it reaches the medulla the lateral cerebellar tract inclines obliquely across the spinal root of the fifth towards the dorsal surface (figs. 136, 137); gradually the other constituents of the inferior cerebellar peduncle apply themselves to it; and its fibres, which retain throughout their remarkable thickness, finally end, after a fairly-simple course, in the vermis. The lateral cerebellar tract is, therefore, an uncrossed path between the posterior roots and the cerebellum. The fact that it degenerates upwards indicates that we are to look upon it as a centripetal conducting system. The lateral cerebellar tract is very early myelinated (in the beginning of the sixth month of embryonic life, *Bechterew*). Some fibres, commonly known as the ventral fibres of the



lateral cerebellar tract, belong, in all probability, to Gowers' bundle, and will be described in connection with it. In the dog, *Pellizzi* finds another and smaller mesial tract, which does not pass over into the corpus restiforme, but enters the cerebellum by way of the brachium pontis above the point of exit of the trigeminus.

Some fibres of this region appear to degenerate downwards also. After the removal of the cerebellum *Marchi* found degenerating fibres throughout almost the whole of the anterior column, and more especially in its peripheral part.

The descending degeneration is explained by *Lenhossék* on the ground of the fork-like division of the fibres where they enter the white substance.

**4. Gowers' Tract.**—This bundle makes its first appearance in the lower lumbar cord, considerably farther down, that is to say, than the lateral cerebellar tract, and increases in size as it advances brainwards. Its fibres probably take origin from cells inside the anterior column of the same side and also (through the anterior commissure) from some in the contralateral column (*Edinger, Guarneri and Bignami, Mott*); they collect together, for the most part, on the periphery of the lateral column, forming, as it were, a continuation of the lateral cerebellar tract. The fibres which have been mentioned as the ventral portion of the lateral cerebellar tract are probably identical with this bundle, which *Gowers* named the ascending antero-lateral column, and *Bechterew* the anterior external lateral-column bundle. It is narrowest near the anterior roots and widens out dorsalwards. Whether it extends beyond the anterior roots to reach the periphery in the sulcus anterior is as yet uncertain.

*Bechterew* places the terminus of this tract in the medulla oblongata; but it is certain that a considerable part of it (in the ape, dog, cat, rabbit, as well as in Man) can be followed farther brainwards, lying to the ventral side of the corpus restiforme and the dorsal side of the olive. This body of fibres pierces the corpus trapezoideum and then proceeds, between the roots of the nervus abducens and nervus facialis, to the region of the corpora quadrigemina. Here it bends round in a loop and streams into the cerebellum. Thus, like the lateral cerebellar tract, Gowers' bundle forms an important connection between the cerebellum and cord. Another part of it seems to ascend still farther brainwards.

Gowers' bundle in the embryo is myelinated in the eighth month, later, that is to say, than any other constituent of the lateral column except the lateral pyramidal tract.

This region of the cross-section frequently degenerates upwards, as, for example, in compression-myelitis; but it seems to be included only at a very advanced stage of the disease (*Francotte*). In cases of tabes with very marked sensory phenomena, ascending degeneration of Gowers' bundle has several times been observed. Some fibres have been found degenerating downwards in this region. *Bechterew* attributes to this tract the function of transmitting sensations of pain.

**5. The rest of the Anterior and Lateral Columns.**—In this paragraph we shall include all those tracts which have not found a place



hitherto. As far as a division into short and long tracts is allowable, we may say that we have here to deal with short tracts, fibres which come out of the grey matter (fig. 116, 21, 22), to enter it again after a short longitudinal course, forming in this way connections between segments of the spinal cord at various heights.

All the several constituents of the cord which are here described can be followed, at any rate, as far as the proximal end of the mid-brain, within the substantia reticularis of the tegment; not that we wish to imply by this statement that each individual fibre has anything like such an extensive course as this; rather are the several tracts made up of fibres frequently disappearing to be replaced by new ones, so that no essential alteration in the cross-section of the tracts need necessarily occur at any particular height.

The ground-bundle of the anterior column is the one most easily followed brainwards. We have already seen that this bundle, *VG*, is a little displaced by the crossing of the pyramids (fig. 132 *et seq.*). Farther forwards the inter-olivary layer made by the crossing of the fillets presses the anterior ground-bundle together with a portion of the lateral column dorsally, the three together forming the substantia reticularis alba (*formatio reticularis medialis*). The most ventral portion of the substantia reticularis alba (the inter-olivary layer) has already been traced upwards in the fillet. The middle portion corresponds to the part of the lateral column just mentioned; to it certain bundles of fibres originating in the nuclei of the posterior column join themselves, while the most dorsal section of the substantia reticularis alba, which is sharply marked off from the grey matter on the floor of the fourth ventricle, is developed from the anterior ground-bundle. It may be mentioned herebefore hand that the middle portion which is formed out of the remains of the lateral column seems to end, above the origin of the hypoglossal nerve, in those grey masses (*nuclei centrales inferiores* of *Roller*, figs. 138, 139, *Nct*) which lie up against the raphe on either side the middle line, and separate the fillet from the continuation of the anterior ground-bundle, *VG*, which henceforth receives the name 'posterior longitudinal bundle.'

**The posterior (or mesial) longitudinal bundle**, *Flp* (fig. 138 *et seq.* and fig. 154), can be followed as far as the anterior corpus quadrigeminum. It forms a bundle, very distinct in cross-section, which lies on either side of the raphe, beneath the grey matter of the fourth ventricle and the aqueduct of Sylvius. Its ventral edge is never sharply defined, for it cannot be separated from the other longitudinal bundles of the tegment with which it mingles. It is very difficult to trace the posterior longitudinal bundle beyond the oculomotor nucleus. A portion of it is supposed to pass over into the posterior commissure.

With regard to the origin and course of the fibres of the posterior longitudinal bundle the greatest diversity of opinion prevails, nor has the question been satisfactorily settled by the recent researches of *Held*, *Cramer*, *Kölliker*, *v. Gehuchten*, and *Ramón y Cajal*. One fact of undeniable importance is that it is myelinated very early, shortly after the root-fibres.



It is also certain that degeneration proceeds both upwards and downwards (nearly to the cervical swelling) in it.

There can be no doubt that it comes into relation with the various nerve-nuclei of the brain-stem, either by receiving fibres from them, or by coming in contact with their cells directly or through collaterals. The most plausible theory is that its fibres take origin in sensory end-nuclei and end (with or without crossing) in motor cells of origin. It would thus represent the simplest form of sensory-motor reflex tract. The existence of collaterals connecting the fibres of this bundle with the nuclei of the oculomotor nerves may be taken as proved. It dwindles rapidly in the region of the oculomotor nucleus; and it is very probable that many of its stem-fibres end there. *Ramón y Cajal* draws attention to some fibres which take origin in the large-celled auditory nucleus (nucleus vestibularis), and, after crossing the middle line, continue their course brainwards in the posterior longitudinal bundle. By giving off collaterals which approach the oculomotor cells, they are supposed to furnish an anatomical basis for the well-known compensatory movements of the eye in vertigo.

The anterior part of the posterior longitudinal bundle appears to arise in a group of large cells situate in the central grey substance of the third ventricle, a little in front of the anterior commissure (nucleus fasciculi longitudinalis superior of *Edinger*). *Kölliker* supposes that a part of the bundle crosses on the dorsal side of the corpus mammillare, while the larger portion is lost on the mesial and ventral side of the red nucleus.

It seems also to receive fibres from other regions, such as the corpora quadrigemina. The fact that its size in cross-section, which represents the sum of the fibres contained in it, is variable, and largest in the middle, points to the conclusion that only a portion of the fibres run through its whole length, and that a great number of short fibres enter into its composition.

It has been asserted that the posterior longitudinal bundle consists chiefly of fibres destined to connect the nerve-nuclei of the eye-muscles. But we see that in the mole, though the oculomotor nucleus is altogether absent, the posterior longitudinal bundle is as well developed as in the rabbit. This has led to a denial that any relation exists between it and those nuclei. In the lizard the posterior longitudinal bundles are very thick and conspicuous, owing to their coarse fibres, and can be followed for the whole length of the cord. They enter into relation with the anterior commissure of the cord.

After removal of one hemisphere of the cerebellum, *Marchi* observed very conspicuous degeneration of the posterior longitudinal bundle of the same side, and in a slighter degree of the contra-lateral bundle. We have as yet no certain knowledge of how this degeneration comes about.

Of the fibres of the remainder of the lateral column we know that they take origin from cells most of which lie in the middle parts of the grey substance of the cord, and bend round, some upwards, some downwards. The greater number of them constitute short tracts, though many fibres



continue their course as far as the medulla oblongata. Here they probably end in those cells in the substantia reticularis alba which *Kölliker* includes under the name of isolated cells of the substantia reticularis. In some places these cells are grouped together, forming the conspicuous masses of grey substance which we have learnt to know as the nuclei centralis inferior et superior and the nucleus of the tegment (*Bechterew*). Thus it comes about that the fibres from the lateral column of the cord, which in lower planes of section yield a large proportion of the longitudinal fibres of the tegment, are steadily reduced in number as they approach the brain and become very scarce by the time the region of the corpora quadrigemina is reached.

In the region of the corpora quadrigemina where the brachia conjunctiva force themselves into the tegment, taking up a great part of its area in Man, only a very small number of longitudinal fibres, as a matter of fact, remain over from the formatio reticularis, apart from the posterior longitudinal bundle and the fillet. An ill-defined small bundle of medullated nerves may be pointed out on the lateral side of the posterior longitudinal bundle, *Fcop* (fig. 149). According to *Wernicke's* researches this bundle bends towards the middle line in front of the corpora quadrigemina, crossing over in the roof of the most anterior portion of the aqueduct of Sylvius. After helping to form the posterior commissure, it reaches the optic thalamus of the opposite side, in which it ends.

Throughout the whole extent of the cross-section of the tegment, the longitudinal fibres, which are early myelinated, run separately or in small bundles only. It must, however, be pointed out that the lateral columns are by no means the only source which supplies these more scattered fibres of the tegment. Their number is increased by accessions, from various quarters, the complement from the central tegmental tract being probably the most important. Numbers of these fibres cross the middle line in the vicinity of the anterior corpora quadrigemina, some near the basis cerebri on the ventral side of the red nucleus (*Forel's* ventral tegmental decussation), others more dorsally beneath the posterior longitudinal bundle (*Meynert's* fontanal tegmental decussation), *F* and *M* (fig. 149).

The fibres here described (under 5) belong almost exclusively to short tracts, so that extensive secondary degeneration is to be looked for only in exceptional cases. The fasciculus intermedio-lateralis alone degenerates a long way down in lesions of the cord. It lies in front of the lateral, pyramidal tract.

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## B. THE CRANIAL NERVES.

In studying the cranial nerves we must first determine in what cell-groups they originate or end. Next, we must try to discover the most important connections which bring these cell-groups into functional relations with other regions of the central nervous system, and especially with the cortex. Strictly speaking, we should restrict the name 'nerve-nucleus' (nucleus of origin) to those groups from which a nerve-root arises in such a way that each single fibre represents the prolonged axis-cylinder processes of a cell. For the sake of a more convenient terminology, we may, however, include the collections of cells in which peripheral (sensory) nerve-roots break up under the title of nerve-nuclei or end-nuclei. The name 'nucleus of origin' must not, however, be applied to them.

**I. Nervus Olfactorius.**—The central apparatus of the sense of smell may be regarded in Man, not only as a relatively feeble organ, the development of which has been arrested, but as an organ affected in the adult by a distinct retrogressive atrophic process in addition to its genetic inferiority. In its want of development it resembles the corpus callosum of lower mammals, which may be almost or completely absent.

Not only is the olfactory bulb in Man undeveloped, but its atrophy is evidenced by the numerous amyloid bodies to be found in the course of the cerebral connections of the adult olfactory nerves.

In studying the central organs of the sense of smell, it is well to employ not only the human brain, but also the brains of animals in which the sense of smell is well developed; *e.g.*, carnivora and rodents.

The olfactory organs are very ill-developed in apes as well as in the aquatic predatory mammalia; in many cetacea, the dolphin, for example, the whole olfactory apparatus is absolutely wanting.

[The nature of the sense served by the olfactory membrane in the several classes of vertebrates offers much room for speculation. In fishes the membrane and its central connections are well developed. In lacerilia and ophidia not only is the olfactory membrane highly organised, but it also presents a further specialised portion, the organ of Jacobson, of much greater sensitiveness than the rest (*Beard*). The relative development of the membrane is fairly constant throughout the four lower classes of vertebrates, whether aquatic or terrestrial; as soon, however, as a mammal takes to the water its olfactory organs dwindle. In the otter they are very ill-developed; in sirenia still more rudimentary; in cetacea they are practically absent in the adult. A consideration of the alteration in character which the sense of smell must undergo to adapt it from a power of appreciating the quality of substances in solution in water, to a power of recognising substances suspended in air, raises a doubt as to whether the sense is fundamentally the same in the two cases. As is well known, the olfactory membrane of the mammal is quite insensible to the action of the most strongly-odorous bodies when presented to it in solution in water. On the other hand, an air-breathing animal, when under water,



would be incapable of using its olfactory organ without such an adaptation of the apparatus as would allow of the renewal of the water in contact with the olfactory membrane without its passing into the lungs. Since this arrangement has not come into existence the olfactory membrane is useless.]

*Broca* and *Turner* divide the mammalia into osmatic and anosmatic animals, according as the sense of smell is well developed, or ill developed or absent.

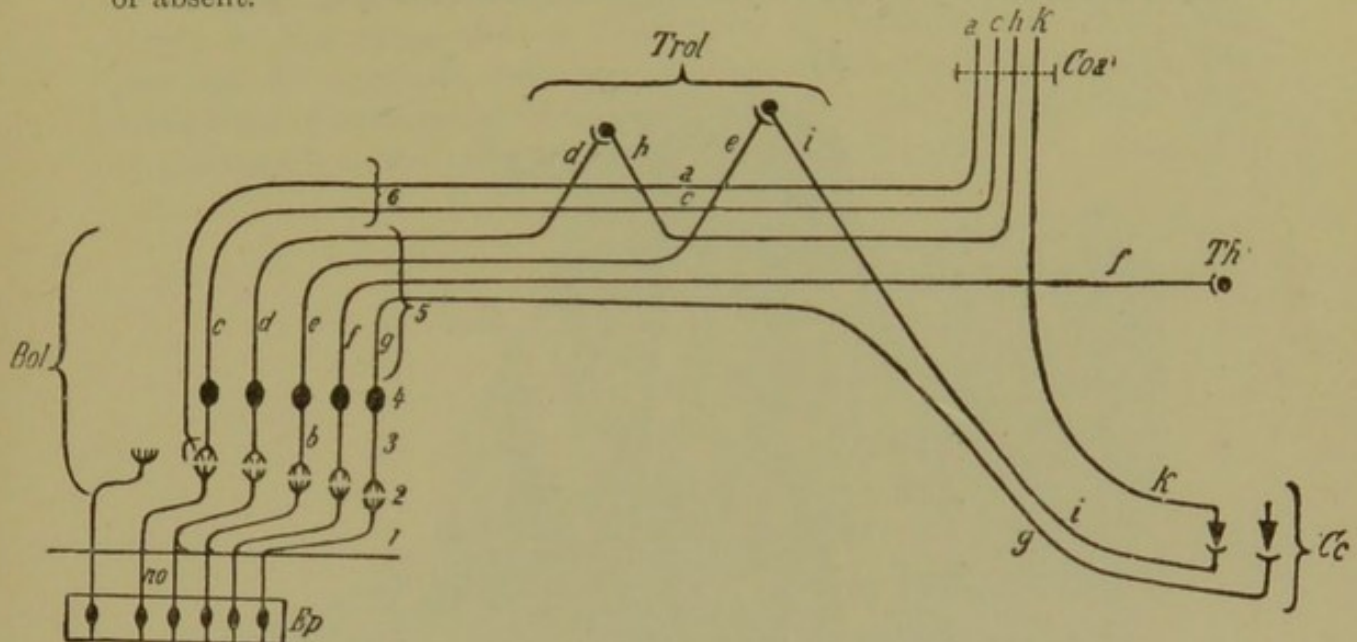


Fig. 159.—Scheme of the central olfactory apparatus.—*Ep*, Olfactory epithelium; *Bol*, bulbus olfactorius; *Trol*, tractus olfactorius; *Coa*, commissura anterior; *Th*, thalamus opticus; *Cc*, cortex of the temporal lobe; 1 to 6, the six layers of the bulbus olfactorius.

The peripheral nerves of smell, *no*, originate in the pigmented region of the olfactory cells of the Schneiderian membrane. The olfactory cells, which lie among the epithelial cells, are very poor in protoplasm, and have two processes; the thicker is short and extends to the free surface of the mucous membrane, the thinner is the central process and passes over into a nerve fibre under the epithelial layer (*cf.* fig. 159, *Ep*). These fibres of the olfactory nerve are non-medullated, and pass through the perforations of the cribriform plate into the interior of the skull-case, where they attach themselves to a greyish-yellow, rounded body of small size in Man, the **bulbus olfactorius**, *Bol* (*caruncula mammillaris*, lobe olfactif), fig. 160.

The olfactory bulb lies on the orbital surface of the frontal lobe, at the front of the sulcus olfactorius. It is free on all sides, with the exception of its attachments to the olfactory nerves, and a strong stalk or peduncle which runs backwards to join with the rest of the brain, the tractus olfactorius, *Trol*.

The fine anatomy of the olfactory bulb is best studied in sagittal sections through this structure in the dog (figs. 161, 162, and 163). On slight magnification we see, if the section runs through the middle of the bulb, *b*, and the tract, *t*, that a fine canal, *V*, traverses the tract almost as far as the front of the bulb. In frontal section this canal



proves to have the form of a transversely-disposed slit (*ventriculus bulbi olfactorii*). It communicates with the lateral ventricle of the brain [by a narrow slit-like opening on the inner side of the head of the *nucleus caudatus*]. The *bulbus olfactorius* covers the tract as with a hood.

The *bulbus olfactorius* exhibits a complicated stratification, the meaning of which is only revealed by stronger magnification (fig. 162), and can

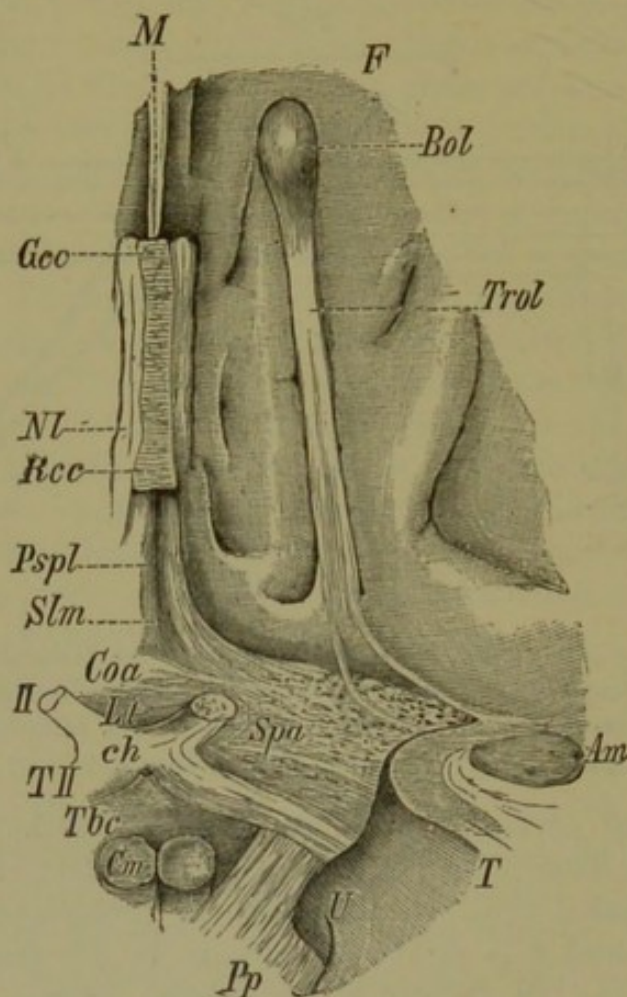


Fig. 160.—A portion of the base of the left hemisphere in front of the optic chiasm. *The apex of the temporal lobe is cut away.*—*Pp*, Pes pedunculi; *Cm*, corpus mammillare; *Tbc*, tuber cinereum; *T II*, tractus opticus; *ch*, chiasma; *II*, nervus opticus; *T*, temporal lobe; *U*, uncus; *Am*, nucleus amygdaleus; *Spa*, substantia perforata anterior; *Lt*, lamina terminalis; *Coa*, bulging forward of the grey commissure of the floor produced by the anterior commissure; *Pspl*, pedunculus septi pellucidi; *Slm*, sulcus medius subst. perf. ant.; *Rcc*, rostrum corporis callosi; *Gcc*, genu corp. callosi; *NL*, nervus Lancisii; *M*, incisura pallii; *F*, frontal lobe; *Bol*, bulbus olfactorius; *Trol*, tractus olfactorius.

be most clearly understood by the application of the silver-method of impregnation (see also fig. 159). First comes the enveloping pia mater, *p*, which does not, however, appear as a continuous layer, as shown in the picture, but is rather torn into many pieces by the numerous olfactory fibres which enter the bulb. Large vessels from the pia mater sink into the bulb. The first nervous layer is made up of the very fine bundles of



the olfactory nerve (1), which after passing the pia mater run, as a rule, some distance in a sagittal direction, so that they are cut across in transverse section.

The second layer (stratum glomerulosum) is already very conspicuous with a low power. It is formed of peculiar globular masses (glomeruli), 0.05 to 0.30 mm. in diameter, fairly closely packed together.

The large vessels which enter from the pia tend to apply themselves closely to the glomerulus to which they give off fine branches. The glomeruli are separated from surrounding structures by a more or less broad layer of granules, of which we know little beyond the fact that they stain intensely by the usual methods of nuclear staining.

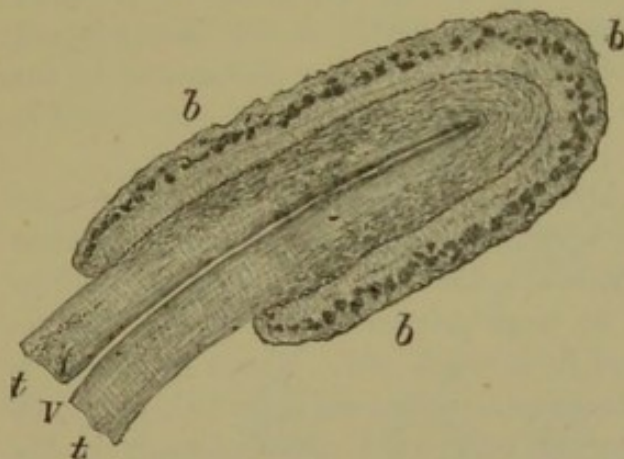


Fig. 161.—Sagittal section of the bulbus olfactorius of the dog. *Magn. 4.*—*b*, Bulbus olfactorius; *t*, tractus olfactorius; *V*, ventriculus olfactorius.

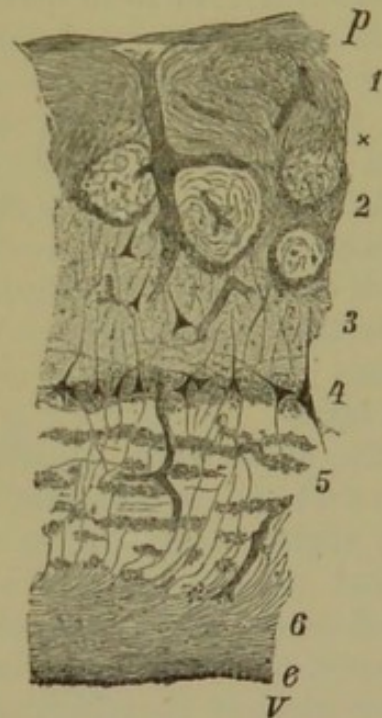


Fig. 162.—Portion of a sagittal section of the olfactory bulb of the dog.—*P*, Pia mater; *1*, layer of peripheral nerve-fibres; *2*, stratum glomerulosum, at *x* fibres are seen streaming out of the first layer into a glomerulus; *3*, stratum moleculare; *4*, nerve-cell layer; *5*, stratum granulosum; *6*, medullary substance; *e*, ependyma; *V*, ventricle.

The staining-methods formerly in vogue showed no differentiation in the glomerulus, so that it was a matter of extreme difficulty to recognise the minute structure of these round bodies. Not rarely (even in carmine-stained preparations) bundles of fibres from the first layer were seen to enter the glomerulus (as at p. 162), but here they were lost in the finely granulated mass which appears to constitute the glomerulus, and in which only scattered nerve-cells are visible.

Only by the silver-method of impregnation is their minute structure revealed. With its aid we see that the olfactory fibres from the peripheral layer enter the glomerulus and break up into richly ramified arborescent



systems. Thus they come in contact with other ramifications belonging to the dendrites of the large nerve-cells of the fourth layer, of which I shall speak later. Each scattered nerve-cell of the third layer also sends a dendrite into a glomerulus. It must not be supposed, however, that only one olfactory fibre enters each glomerulus, for quite a little bundle is assigned to each. Apart from direct demonstration (which is not always easy in silver preparations), this follows from the circumstances that the fibres far outnumber the glomeruli. The third layer or stratum moleculare (stratum gelatinosum), 3, is about 0.3 mm. thick. Here we find some fibres which radiate upwards from the medullary nucleus of the bulb. Some of these lose the myelin-envelope in this layer, others reach the glomeruli and net them round on the under side (fig. 159, *a*). This layer is also permeated by the dendrites (of which mention has been made before) which extend to the glomeruli from the cells of the fourth layer (fig. 159, *b*). In the inner part of this layer (fig. 163, *3 b*) we see a close network consisting entirely of protoplasmic processes. They belong to cells of the fourth layer, and to the small cells of the fifth. The cell-elements we meet with here are medium-sized nerve-cells, triangular or fusiform, which strike their axis-cylinder processes downwards to the deeper layers, while their dendrites enter into the composition of a glomerulus in the fashion just described. A number of scattered granules are also found in this layer.

The fourth layer, 4 (nerve-cell layer), constitutes a thin sheet, not more than 0.04 mm. in thickness, which appears in carmine preparations, when only slightly magnified, as a dark line. This layer consists of thickly-packed granules, amongst which lie large triangular nerve-cells, the so-called mitral cells, usually arranged in a single row. These cells have a diameter of 30 to 50  $\mu$ ; their axis-cylinder processes (figs. 159, *c, d, e, f*), course straight inwards, and sooner or later bend round (usually in the fifth layer) and assume a longitudinal course. Each gives off a number of collaterals, which are said to run back into the molecular layer. In the protoplasmic processes of the mitral cells we observe a varied disposition. Some of them take a horizontal course, fork again and again, and take part in the composition of the deep-lying feltwork of fibres in the molecular layer (*3 b*). Often they can be followed for a considerable distance. One protoplasmic process, however, always lays claim to special attention. It passes outwards through the molecular layer, rarely giving off side-branches, and in the glomerulus suddenly breaks up and ends in an extraordinarily rich plexus, the branches of which are interwoven with similar ramifications of olfactory fibres (*cf.* fig. 99, *4*). In the dog each mitral cell has usually a single process of this character.

The behaviour of the dendrites of the mitral cells varies very greatly (as we shall learn) in different animals, according to the degree of development in their sense of smell.

The next layer, stratum granulosum, 5, which is not marked off sharply from the sixth, is broadest at the apex of the bulb (1 to 1.5 mm. in diameter in the dog); towards the hinder end it gradually disappears



altogether. It is especially characterised by its closely-packed granules arranged in several rows parallel to the surface, between which bundles consisting largely of medullated nerve-fibres, most of which take origin in the mitral cells, course in the same plane. This layer is in addition pierced by a number of radiating medullated fibres, which coming out of the medullary layer of the bulb lose their myelin, some in this layer, some (as already mentioned) in the third layer.

By means of the silver-method of impregnation we can see the singular behaviour of the granules of this layer. They possess a dendrite or dendrites directed towards the centre, and a single dendrite directed towards the periphery. The former divide after a course of varying length, while the peripheral process courses undivided and almost in a straight line to the

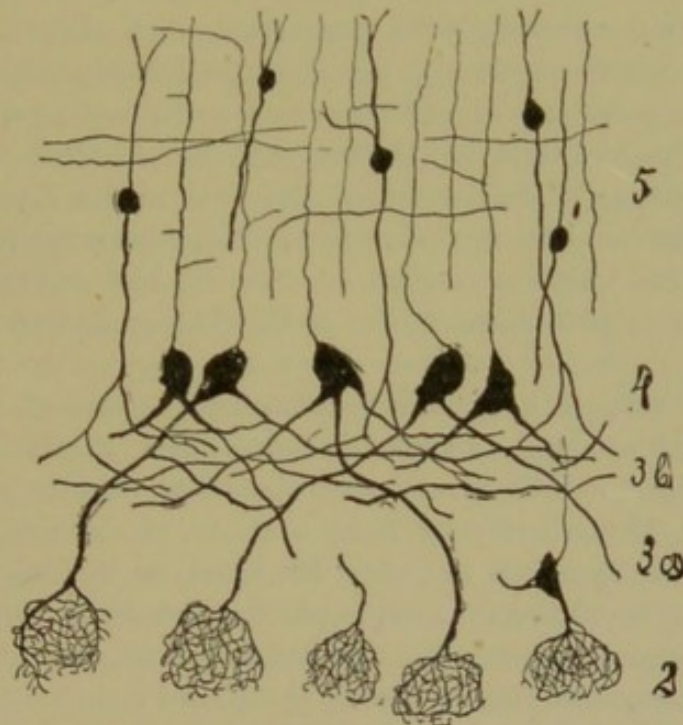


Fig. 163.—From the bulbus olfactorius of the mouse. *Silver preparation*.—2, Glomeruli; 3a and 3b, molecular layer; 4, layer of large mitral cells; 5, granular layer.

deepest parts of the molecular layer, where, near the mitral cells, it splits into several branches, most of which run horizontally. It thus takes part in the composition of the felt-work already referred to, in the deepest part of the molecular layer (fig. 163, 3b). It is very difficult to exhibit the axis-cylinder processes of these cells. *A. Hill* has shown that they either course directly towards the medullary layer or else run peripheralwards as far as the mitral cells, and then bend round towards the deeper parts. [The disposition of the axis-cylinder enables us to divide the granules into two classes: (a) those with much looped axis-cylinders, which give off many lateral branches; and (b) those with unbranched centrally running neuraxons. The granules of the former class are larger than those of the latter.] It is not yet certain that all the cells of the granular layer are alike in behaviour. Single large nerve-cells, especially of the kind known as



Golgi's, are also found in this layer. [Occasionally cells whose processes extend tangentially for a great distance are to be seen. To these the *translator* has given the name of 'bracket-cells.' The thick dendrites of one observed in an adult cat extended right and left for a distance of more than 3 mm.]

The innermost, or sixth layer (6), the medullary centre of the bulbus olfactorius, consists of nerve-fibres which run parallel to one another with a somewhat undulating course. This layer gives off at right angles fibres to the superficial layer, and so diminishes towards the apex of the bulb in the same proportion that the fifth layer grows in thickness. It is limited towards the ventricle by an ordinary ependyma, *e*, with ciliated epithelial cells. In full-grown animals the processes of these cells can be followed far down into the substance of the bulb.

In the human olfactory bulb, nerve-fibres and glomeruli are present. The third and fourth layers are not sharply defined; genuine nerve-cells occur but very sparsely. The granular and medullary layers are distinctly recognised. The ventricle is wanting, but its situation is indicated by gelatinous substance in the centre of the bulb. The layers above mentioned are found on the ventral side of this gelatinous substance only; usually the dorsal portion consists of nothing but medullary substance. For the rest, a minute examination of the human bulbus has yet to be undertaken.

In animals with a keen and well-developed sense of smell the peripheral process of a mitral cell goes in most cases, if not invariably, to a single glomerulus; indeed, several such dendrites (five or six in the dog, according to *v. Gehuchten*) may form a single glomerulus, while, on the other hand, where the sense is feebly developed, as in birds, not only does the mitral cell give off several such dendrites, but the dendrites themselves divide, each mitral cell thus supplying a number of glomeruli (as many as twenty sometimes, according to *Ramón y Cajal*).

[The similarity between certain of the elements contained both in the retina and olfactory bulb has attracted the attention of several anatomists; but it appears to the *translator* that the homology is much deeper than has been hitherto supposed, and that both similarities and differences throw a great deal of light upon the morphology of the central nervous system. It is difficult at the first moment to recognise the homology of the 'nuclei' of the retina, the 'granules' of the bulb, the 'cells' of the ganglion spirale of the ear, and the 'cells' of the ganglia on the posterior roots of the spinal nerves; but it might on *a priori* grounds be supposed that the same plan would be adopted in the connection with the central nervous system of all sensory nerves; and certain considerations with regard to the development of the nervous system give the key to this plan.

The nervous system is first formed in the animal kingdom as a connection between certain cells on the surface, well situate for the purpose of acquiring information with regard to the environment, and contractile, muscular cells, or cell-processes, the action of which adapts the animal



to its environment. The specialisation of spots on the surface into sense-organs is due to the favourable position of these spots and to the sensitive character of the cells, whether pigmented or containing crystals of carbonate of lime, or otherwise adapted to receive impressions. When these cells are collected into sense-organs they need long filaments to connect them with the contractile elements. Further than this, as soon as the cells of the sense-organ are able to distinguish between impulses of different strength and kind, a mechanism is needed for the purpose of distributing the impulses they receive. These distributive cells or nerve-cells are derived, as *R.* and *O. Hertwig* have shown, from sense-cells, which, having lost their receptive properties, have sunk down from the sense-organ into the subjacent mesoblast, and serve henceforth for the distribution to appropriate muscles of the impulses received from their more favoured sisters. The central nervous system consists, in the first instance, of clumps of deposited epithelial cells and the plexus formed by their processes; the clumps lie, therefore, immediately beneath sense-organs.

The next step in the evolution of the nervous system consists in its withdrawal in part to a more central sheltered situation. Its local origin is always marked, however, by the presence of nerve-cells in the vicinity of the sense-organs (the nose, the eye, the ear), or the situation formerly occupied by sense-organs (neighbourhood of the spinal ganglia).

The central connections of the nose and the eye differ from those of the more posterior sense-organs. Less of the nervous labyrinth has been withdrawn from its original local situation in the neighbourhood of the sense-organ, to take part in constituting a cerebro-spinal axis, than in the case of the ear and segmental organs corresponding to the spinal ganglia. In the olfactory bulb and retina are found granules, plexus (glomerular or molecular substance), and associating nerve-cells. In the ganglion spirale and spinal ganglia, bipolar cells alone are found, the plexus or molecular substance (substantia Rolandi) and associating cells (? cells at the base of the posterior horn) being withdrawn into the axis.

This is not merely a morphological speculation. It is hopeless to attempt to trace the central connections of the olfactory and optic tracts until the relation of the nervous elements in the bulb and the retina to the rest of the cerebro-spinal axis has been determined.

Looking at the nervous system from the *translator's* point of view, it is seen to be composed of sense-organs and grey matter, united by nerve-fibres. Processes of the cells of the grey matter stretch out to and innervate muscle-fibres. The grey matter is essentially a plexus providing alternative routes for impulses originating in the sense-organs. In it several different kinds of elements are found. The basal processes of sense-cells never terminate directly in the plexus, but first pass through intermediary neurons; granules in the case of the olfactory bulb and retina, cells of the spinal ganglia in the case of the organs of common sense. On leaving the intermediary cells they break up into a plexus, the processes of which are associated into nerve-fibres by nerve-cells.]

In man the pedunculus bulbi or **tractus olfactorius**, *Trol* (called



formerly, by mistake, the olfactory nerve), which runs backwards towards the substantia perforata anterior, *Spa*, is essentially triangular in form.

The transverse convolution immediately in front of the anterior perforated space (which belongs to the orbital surface of the temporal lobe, and to which the tractus olfactorius is affixed) is also termed the tuber or trigonum olfactorium. The free basal layer of the tract consists of white matter; its upper angular portion embedded in the sulcus olfactorius rises abruptly behind, and blends with the mesial wall of this sulcus (superior olfactory root). Another convolution passes from the tractus obliquely backwards and outwards, closes in this sulcus posteriorly, and determines the triangular form of the convolution known as the trigonum.

The shape of the cross-sections of the tract in Man varies greatly during its course; in the anterior half it is, as a rule, triangular with rounded corners and slight concave sides (fig. 164).

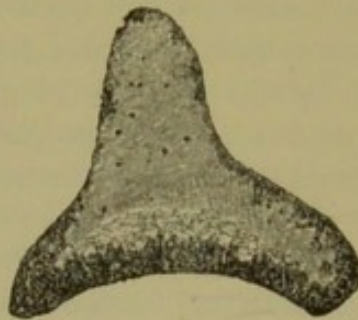


Fig. 164.—Transverse section of the human olfactory tract. *Glycerin preparation.*  
*Magn. 15.* The bundles of nerve-fibres appear dark.

A layer of fine medullated nerve-fibres, about 0·3 mm. thick, occupies the basal surface and extends round the lateral angles. It can often be divided into two layers of nearly equal depth, the superficial one is closely packed with nerve-fibres, while in the deeper they are more thinly dispersed. Next follows a layer, 0·1 to 0·3 mm. thick, which consists for the most part of gleia and corresponds to the obliterated ventricle, while all the rest of the tract is derived from modified cortex. On its dorsal surface it is covered by a distinct stratum of medullated nerves, and it contains small, irregularly disposed nerve-cells which are more numerous and more definitely pyramidal towards the hinder end of the tract. In almost all adults, and especially in old people, the basal nerve-layer contains numerous amyloid bodies. The middle layer, which corresponds to the ventricle, may be completely filled with these bodies, while, at the same time, the cortical layer also shows them in smaller numbers and almost exclusively in the white stratum. Their presence enables one to trace the olfactory tract in its further course, especially after staining with alum-haematoxylin or after rapid dehydration (*Tuczek*).

In osmotic mammals we find at the base of the brain a massive lobe, the lobus olfactorius, which carries the bulbus olfactorius on its anterior end, and, widening out behind, blends with the anterior part of the



temporal lobe. With the adjoining parts of this latter it forms a pear-shaped swelling, the lobus pyriformis. In sagittal sections coloured by methods of medullary-sheath staining it is seen that a not inconsiderable number of fibres, in their course backwards (fig. 159, *d*, *e*), enter the grey cortical layer of the tract, *Trol*. This also is, therefore, a cortical centre for many olfactory fibres. Such preparations also show fibres which coming out of the cortex of the tract (*h*, *i*) turn backwards towards the brain and so represent the fibres which, having originated in the bulb, made their way into the cortex.

At the hinder end of the human brain the superficial visible white fibres of the olfactory tract also separate into several bundles, all of which course outwards and backwards, the outer or **lateral olfactory root**. One of these bundles, the most lateral [*stria externa*], is always distinctly visible; it disappears in the gyrus uncinatus, near the nucleus amygdaleus, *Am*. Of the other bundles one or more, not always distinct, pass outwards and backwards, skirting close by the large holes of the substantia perforata; they cannot (with the naked eye) be followed into the temporal lobe.

No white **mesial root** [*stria interna*], as commonly described, is to be seen on the surface in Man; but by analogy with the internal olfactory root of osmotic animals, this name is applied to the region of the cortex which lies between the tuberculum olfactorium on its mesial side and the lower end of the gyrus fornicatus, and in the depth of which a fibre-tract is actually to be found. Neither does a middle grey root, in the common meaning of the term, exist.

In the brains of old people, we are able with the help of the amyloid bodies to follow the course of the olfactory tract farther back on the free surface of the substantia perforata anterior. Amyloid bodies affect especially the lateral white root. It is possible to follow this root some distance beyond the substantia perforata into the brain-substance on both sides of the corpus striatum. On the lateral surface of this nucleus we meet with a quantity of large, round, or spindle-shaped cells almost completely filled with light yellow pigment, 30 to 60  $\mu$  in diameter. They, too, are probably to be reckoned to the central apparatus of olfaction.

In addition to the roots already mentioned, a bundle (*a*, *c*, *h*) extends from the tractus olfactorius towards the anterior commissure.

The **anterior commissure** (*a*, *c*, *h*, *k*), may be looked upon as partly supplementary to the corpus callosum. Its function is to unite together points on the two hemispheres, mainly, but by no means invariably, identical. It provides for those portions of the cortex which are not supplied by the corpus callosum. It is, in the first place, a commissure (perhaps, also, a decussation) between the rhinencephali of the two hemispheres. A bundle, well-developed in osmotic animals but rudimentary in Man, goes from the cortex of the tractus olfactorius (inclusive, perhaps, of the trigonum), and, crossing the middle line in the anterior commissure, unites with the corresponding bundle on the other side to form an arch, concave in front (the pars olfactoria). There is also present in Man a slender tract of fibres which, separating from the bundle which



passes towards the anterior commissure, streams into the under border of the internal capsule and so reaches the front of the optic thalamus. A direct connection may also exist between the bulbus olfactorius and the anterior commissure. Thus *Kölliker* supposes that the medullated fibres which extend into the molecular layer and to the glomeruli, and there break up (fig. 159, *a*), come by way of the anterior commissure. According to *Löwenthal*, they take origin from the contra-lateral lobus olfactorius.

In Man the hemispherical portion of the anterior commissure (*pars temporalis*, *k*) is by far the more important. It forms an arch, concave behind, the sides of which (figs. 152, 153, *l*) turn backwards and downwards, and run into the temporal lobe, wedged in, as it were, at the base of the nucleus lenticularis, between the putamen and globus pallidus. What portions of the cortex they ultimately reach remains at present undetermined. The main source of the anterior commissure was said by *Popoff* and *Flechsig* to be the gyrus lingualis, but the observations of *Henschen* and *Déjerine* are opposed to this conclusion. A portion of the fibres from the anterior commissure enters the external capsule.

On the ground of *Ganser's* experiments it was also assumed that the anterior commissure contains commissural fibres alone and no decussating fibres [of the olfactory tract], but this opinion has been somewhat shaken of late.

The cortex of the cornu Ammonis must also be reckoned among the central olfactory organs, and the psalterium (see p. 82), the massive commissural system which stretches between and connects the cornua of the two hemispheres, ought therefore to be treated of here, as ought also the fornix. In the interest of simplicity, however, I prefer to reserve the full discussion of these structures till later, and to content myself, in this place, with merely mentioning their connection with the sense of smell.

Four kinds of medullated fibres, at least, may, therefore, be distinguished in the olfactory tract:—

(1) Those from the mitral cells of the bulb to the cortex of the tract (fig. 159, *d*, *e*).

(2) Those from the mitral cells of the bulb which run in the tract, without coming into connection with its cortex, backwards towards other portions of the cortex (*g*), or to non-cortical ganglia (*f*), especially the thalamus opticus (*Tho*).

(3) Fibres from the anterior commissure which end either in the bulbus or in the cortex of the tract, or take origin from the cells of the latter (*a*, *c*, *h*).

(4) Fibres from the cortex of the tract which run to other parts of the cortex or elsewhere in the brain (*i*).

It cannot be stated whether the very strong root of the olfactorius which passes to the nucleus amygdaleus and cornu Ammonis, consists of fibres of class 2 or class 4.

A tract of fibres (fig. 160, *Pspl*), or, to speak more exactly, an atrophied and modified part of the cortex, pedunculus corporis callosi (pedunculus



septi pellucidi, gyrus subcallosus), which extends from the apex of the rostrum corporis callosi obliquely backwards and outwards across the substantia perforata anterior towards the tip of the temporal lobe, is to be reckoned in with the central olfactory apparatus. This tract was first described by *Broca* as "la bandelette diagonale de l'espace quadrilatéral." It is only exceptionally demonstrable in Man, in atrophied brains, as, for example, in old persons, and in dementia paralytica.

In many animals, however, such as *Histrix* and *Dasypus*, this tract attains very large dimensions (*Zuckerkanndl*). The bundles of which it is composed belong to an association system peculiar to the olfactory nerves, the olfactory bundles of the cornu Ammonis (*Zuckerkanndl*), which can be rightly studied and understood only in the brains of osmotic animals. It consists of fibres which run in the body of the fornix as far as the posterior border of the septum pellucidum, where they become distinct from it (processus olfactorius fornicis, *Zuckerkanndl*) and turn downwards in front of the anterior commissure towards the base of the brain. Arrived there, they assume a lateral direction, and stream, some into the temporal, some into the olfactory lobe. It is with the former, the fasciculus hippocampi (*Zuckerkanndl*), that we are chiefly concerned at present.

Many attempts have been made to distinguish as an independent region of the cortex (rhinencephalon) those parts which are directly connected with the olfactory organs.

The central terminus of the olfactory tract may be looked for in the subjoined regions:—(1) The cortex of the tractus olfactorius, the tuberculum olfactorium, and (in animals) the lobus pyriformis. (2) The cortex of the gyrus hippocampi and cornu Ammonis. To this can be added, in all probability, the anterior end of the gyrus fornicatus, as well as, perhaps, the nucleus amygdaleus.

The extent to which the cornu Ammonis is in intimate physiological connection with olfactory centres, is shown by the fact that it is quite rudimentary in the dolphin (*Zuckerkanndl*) [and all other cetacea], and small in Man; whereas in animals with well-developed organs of smell it is large, and runs in company with the fornix far beneath the corpus callosum.

A comparison of the brains of carnivorous animals shows a very striking development of the temporal lobe in those which track their prey and detect the proximity of danger by the sense of smell, as compared with those which rely upon other senses. Until the typical form of brain cortex has been agreed upon, we are in no position to judge of the minute structure of the cornu Ammonis. Of the lobus pyriformis, it may be observed that very curious nerve-cells (double pyramidal cells) are found in the superficial layer of the cortex. They give off two very conspicuous dendrites, with tuft-like ends, which proceed in opposite directions, one to the centre, the other to the periphery. *Kölliker* was able to follow the axis-cylinder process of these cells to the neighbourhood of the outer capsule. There is no question that the whole olfactory region is marked by characteristics peculiar to itself.



The investigations of *Calleja* have proved that all the fibres which proceed from the olfactory bulb and tract to the various parts of the cortex end in the upper molecular layer, where their arborescent systems mingle with the protoplasmic ramifications of the deeper-seated pyramidal cells, *Cc*.

*Edinger* has shown that phylogenetically the olfactory nerve sends tracts to the superior cerebral centres earlier than any other. In amphibious animals, especially reptiles, which have not otherwise attained to a developed cortex, these olfactory connections light upon a well-developed brain-cortex, corresponding in character and position to the cornu Ammonis.

The gyrus fornicatus and the gyrus hippocampi together form a great arch on the mesial wall, its lower and anterior end closed by the lobus olfactorius. *Broca* included this whole arch in the cortical field of smell, and named it the lobus limbicus. It is probable, however, that the greater part of the gyrus fornicatus (which is well developed in Man) has other functions. We could more readily suppose that in Man the fascia dentata and nervus Lancisii answer to the atrophied lobus limbicus.

We may say, then, that in the olfactory region impressions are received by the olfactory cells (fig. 159, *Ep*) and conveyed by the olfactory nerves (*no*) to the glomeruli (2), where they are transmitted to neurons of the second class. These latter consist of the mitral cells (4) with their principal dendrites (*b*) and their axis-cylinder process, which conveys the impression along the path marked *f* to the thalamus, or along that marked *g* to the cortex, *Cc* of the temporal lobe. To the commissural fibres *Kölliker* assigns the task of maintaining the harmonious working of the olfactory central organs in the two hemispheres. No profounder physiological interpretation of the conditions just described has as yet been suggested. We are, for example, quite in the dark as to the meaning of the granules.

The fibres (*f*) of the olfactory tract which end in one of the central cerebral ganglia (usually the thalamus opticus), though not yet fully understood, are certainly of essential importance. They are homologues of the fibres of the fillet, being sensory neurons of the second class and ending in the mid-brain; and we may therefore assume that the greater number of them cross in the anterior commissure.

The lobus olfactorius originates as an outgrowth of the lateral wall of the fore-brain, and bears traces of the central cavity even in Man. The bulbus is a secondary accretion.

When we consider that sensations of smell, of taste, and of touch, as conveyed by the trigeminal nerve, are almost capable of being fused into a single perception in a way which is not possible with the other senses, such as sight and hearing, we are prepared to believe (although direct anatomical proof is not yet obtainable) that the cortical terminations of the olfactory trigeminal and glossopharyngeal nerves either lie in the same neighbourhood or are, at any rate, very intimately connected by associating fibres.

[A consideration of the almost exclusive part played by sensations of



smell in the daily life of most carnivorous animals would prepare us to expect that a very large portion of the cortex of their brains must be devoted to their reception. If the brains of a large number of different carnivores, such as are exhibited in the fine collection in the Hunterian museum, are compared together, it is obvious without need for measurement that the temporal lobe is very much larger in the dog, wolf, jackal, and other animals which track their prey with the nose, than in other mammals. Felines detect the proximity of their victims in forests and jungles rather by listening for broken twigs and crackling leaves and sticks than by sniffing along their trails; in carnivores of this habit, which might be distinguished as 'springing' animals, the temporal lobe projects forwards to a less extent than it does in the 'running' hunters. A comparison, however, of the aquatic otter with its terrestrial congeners is most instructive. The otter trusts to its sensitive whiskers for guidance amongst the snags and stones in the pools of brown water which the salmon frequent. Its sense of smell is extremely deficient, and, corresponding with this, its temporal lobe is reduced to very small proportions.

Herbivorous animals rely upon their sense of sight for safety. As far as possible they feed in open ground, keeping watchful guard. Doubtless they quickly discover any taint in the air when their enemies depart so far from their usual practice as to hunt from windward, but the use which they make of the nose to escape the enemy is not comparable in intensity or specialisation to the following of a trail which crosses and recrosses countless other lines of scent. On the other hand, they make selection of favourite herbs, and avoid poisonous ones with the aid of smell; so that the difference between the two classes of vegetable and animal feeders is one of degree rather than of kind; whilst carnivores are 'osmotic' *par excellence*, herbivores cannot be justifiably termed 'anosmotic.' Indeed these terms are more likely to lead to confusion than to introduce order. Man, some quadrumana, and all marine mammalia are very deficient in olfactory apparatus. The sense of smell varies greatly amongst remaining mammals. But while it is impossible to speak in antithetical terms of the two divisions into which, from this point of view, they fall—the predatory and the preyed-upon—as, the one, osmotic, and, the other, anosmotic, the relative preponderance of smell-perceptions as a substratum of mental processes must be very different in the two groups. Nor is it difficult to recognise the brain-characters upon which this difference depends. In carnivora the fissure of Sylvius is very oblique, and its margins are pressed close together; the temporal lobe projects a long way forwards beneath the frontal. In herbivora the fissure of Sylvius is more nearly vertical; its margins fall quickly apart, sweeping away from one another in easy curves; the temporal lobe does not project forwards. It is curious to notice the intermediate position taken up by the brain of the omnivorous root-hunting pig.

A study of the comparative anatomy of the brain throws much light upon questions of cortical localisation, and will probably be the ultimate tribunal to which all experimental evidence will be submitted. The



outlines of the three brains given below (figs. 165, 166, 167) are tracings taken from the drawings in Gratiolet's atlas (published before localisation of function in the cortex was thought of), reduced by the pantograph to about the same size. They show the relative development of the temporal lobe in animals with an acute, moderate, and feeble sense of smell respectively.

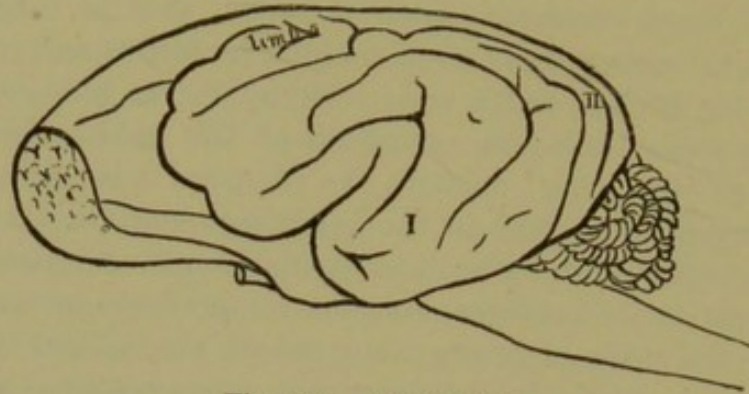


Fig. 165.—Brain of dog.

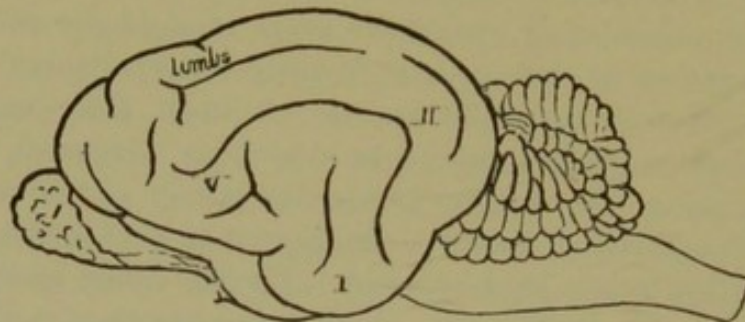


Fig. 166.—Brain of cat.

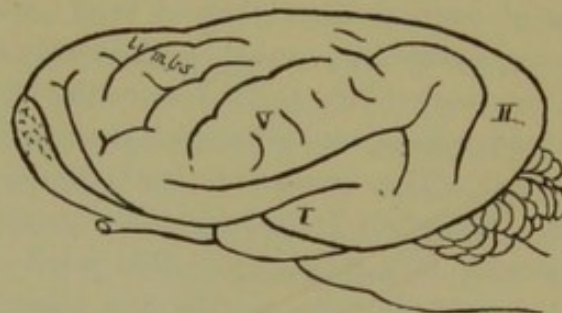


Fig. 167.—Brain of otter.

Tracings of the pictures in Leuret and Gratiolet's Atlas. The Roman numbers indicate approximately the cortical areas, the development of which in different animals varies as the cross-section of the several sensory nerves, to which they correspond.

*Broca* included the gyrus fornicatus in the cortical field of smell. That this is an error is shown by the fact that the gyrus fornicatus is well developed in the marine mammalia.]

Absence of the olfactory tract on one or both sides has been repeatedly observed in otherwise normal brains.

*Kundrat* associates together all forms of defect of the olfactory nerves under the name of arrhinencephalia, allowing, however, that other extensive defects in the structure of the brain are associated therewith.



**2. Optic Nerve.**—There are no peripheral nerves of sight in the proper sense of the word; even the exceedingly short fibres which lead from the rods and cones of the retina (the peripheral terminal organ of the visual apparatus) to the bipolar nerve-cells which also lie within it, are homologous to the posterior roots and their continuation within the cord. The nerve-cells of the retina, as well its deeper parts and the fibres which originate in it, must be regarded as parts of the central nervous system. As is well known, both retina and optic nerves originate from a vesicular outgrowth of the fore-brain, which appears very early in development (primary optic vesicle). The column of fibres which constitutes the optic nerve differs from a peripheral nerve in that, if it is cut, its two ends will never grow together. This appears to be a differential character of all central tracts of fibres.

We will not in this place treat of the minute structure of the retina (fig. 168, *R*); but will confine our attention, in the first instance, to the optic nerve which is composed, for the most part, of axis-cylinder processes of the multipolar cells in the nerve-cell layer of the retina, whence it takes origin. Some fibres which enter into its constitution originate in the brain and end in the retina; these can be distinguished by their extreme fineness. They are few in number, and may exercise a direct or indirect effect upon the nervous elements of the retina in the act of vision. The nerve leaves the orbit as a round column, flattening out a little after it has entered the *cavum cranii*. It runs towards the *basis cerebri*, and forms, in front of the *tuber cinereum*, the optic chiasm with the nerve of the opposite side, *Ch* (figs. 10 and 15). From the optic chiasm the 'optic tracts,' *Tro*, extend backwards and outwards. According to *Salzer's* measurements, the optic nerve of Man has an average cross-section of about 9 sq. mm., reduced to 8 sq. mm. by deducting the space occupied by connective-tissue septa. The number of nerve fibres averages about 438,000, a number which can only be understood if their great tenuity is borne in mind.

The optic nerve-fibres are collected into irregular bundles, round or polyhedral in form, which are separated from one another by thicker or thinner septa derived from the sheath of pia mater which surrounds the nerve. Secondary septa, rich in nuclei, enter the substance of the separate bundles.

At first the bundles destined for the macula lutea lie together in a sector of the *nervus opticus*, the apex of which reaches nearly to the centre of the nerve in cross-section, while the base occupies its lateral border. In sections nearer the brain this field, the papillo-macular region, shifts its position to nearer the centre of the nerve. The papillo-macular fibres, destined for a small but most highly sensitive portion of the retina, take up almost a third part of the whole cross-section. It is probable that fibres which serve the purpose of conveying impulses to the centre for pupillar movement lie in the optic nerve, as well as those intended for actual optic excitation.

The peripheral bundles which lie nearest to the pia, as well as the central bundles which border the *arteria centralis*, invariably atrophy to



such an extent that their fibres are found (except in new-born children) to have completely disappeared; only the empty supporting connective-tissue remaining behind (*E. Fuchs*).

The chiasma opticorum at the base of the brain is formed by the junction of the two optic nerves (fig. 168).

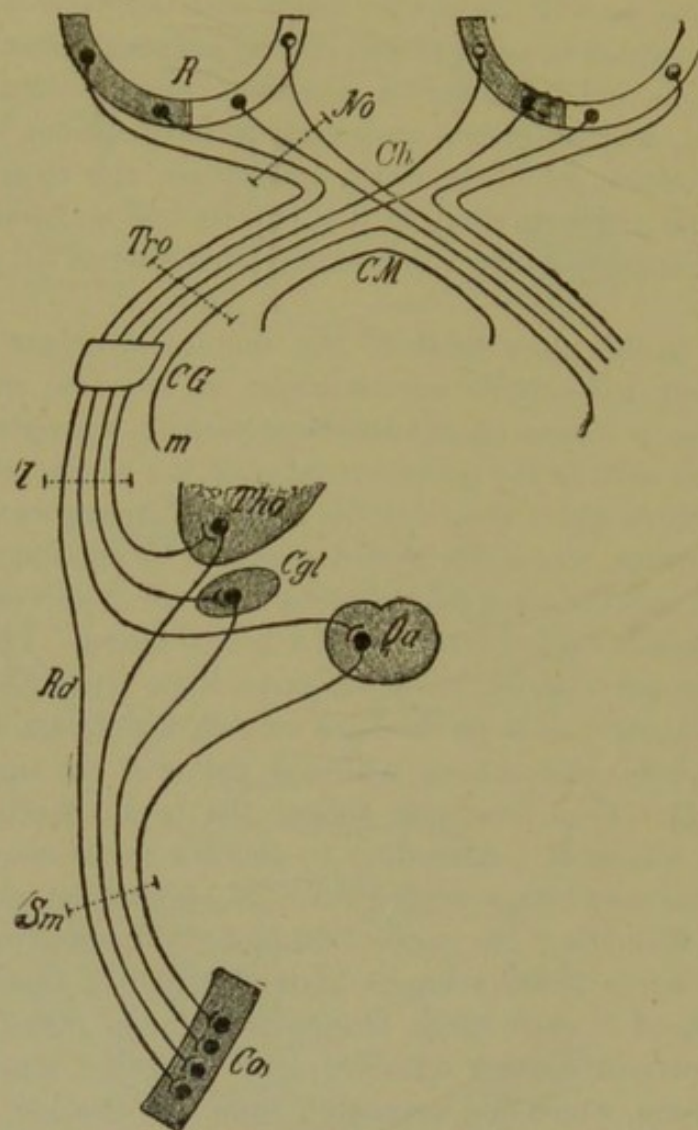


Fig. 168.—Scheme of the central apparatus of vision.—*R*, Retina, dark on the side connected with the left, light on the side connected with the right hemisphere; *No*, nervus opticus; *Ch*, chiasm; *Tro*, tractus opticus; *CM*, Meynert's commissure; *CG*, Gudden's commissure; *l*, lateral division of the tract; *m*, mesial division of the tract; *Tho*, thalamus opticus; *Cgl*, corpus geniculatum laterale; *Qa*, anterior tubercle of the corpora quadrigemina; *Rd*, direct cortical root; *Sm*, sagittal fibres of the corona radiata to the occipital cortex [optic radiations]; *Co*, cortex cerebri (of the cuneus).

It is beyond doubt that there are three kinds of fibres in the optic chiasm:—

(1) Fibres from the lateral halves of the retinae, which occupy the lateral borders of the chiasm, and go to the optic tract of the same side.

(2) Fibres from the mesial halves of the retinae, which cross in the chiasm to the tract of the opposite side.

(3) Fibres which occupy the back of the commissure and extend from



one tract to the other. They are distinguished by their fineness, *CG*, Gudden's commissure (commissura inferior, commissura arcuata posterior).

Even if other kinds of fibres are present in it, the three kinds just mentioned constitute the bulk of the chiasm. The existence of an anterior commissure, lying, as has been supposed, in the anterior angle of the chiasm and connecting the two retinae (*Hannover*), is very improbable.

The relation to one another of the crossed and uncrossed portions of the tract varies exceedingly in different animals. It appears that in Man the uncrossed fibres preponderate, whilst in the lower mammals more crossed fibres are present. In many fishes uncrossed fibres are totally wanting. In birds and mice all the fibres cross; while only a part of them cross in the rabbit, horse, dog and cat. In the rabbit, indeed, the uncrossed fibres are in the minority (*Singer* and *Münzer*). In the mole the optic nerves are rudimentary, and contain only a few poorly medullated fibres; the white inferior commissure is consequently very obvious.

In Man and other mammals the interweaving of the fibres in the chiasm is so intimate and complicated that very little light is thrown upon their relations by making sections; the degeneration-method first helped to clear the matter up. *Ganser* delineates a human brain in which the uncrossed bundle on the right side runs from optic tract to optic nerve as a distinctly isolated column.

In lower animals, and especially in fishes, the nerves cross in coarse bundles. In many fishes the optic nerves simply lie across one another without entering into a chiasm at all. In *Bdellostoma* (a variety of cyclostome) alone, of all vertebrate animals, are the optic nerves absolutely uncrossed.

The **optic tract**, *Tro*, starts from the chiasm. At first it lies close up against the grey basal substance of the brain, but subsequently it rests upon the crus cerebri, around the most anterior free portion of which it winds.

In the chiasm the papillo-macular fibres take up their position on the dorsal side, where they remain throughout the tract, lying next to the base of the brain. The uncrossed papillo-macular bundle is probably in direct contact with the brain substance.

Most of the uncrossed fibres in the brachium opticum have a somewhat complicated course; a large proportion soon pass behind the chiasma to reach the mesial side of the tract.

The myelination of the optic nerve and tract begins only just before birth, so that the optic fibres of new-born animals contain very little myelin. The development proceeds from the centre to the periphery, and at birth hardly extends to the bulbus oculi.

We have already seen that in the visual organs the sensory neurons of the first class end in the nerve cells of the retina, and that the optic neurons of the second class start from the latter. We must therefore rank these cells with those of the posterior columns, and see in the optic nerve, the chiasm, and the tractus, the homologue of the mesial fillet and the decussation of the fillet. To complete the correspondence, most of the



optic fibres end (as we shall learn), like those of the fillet in the ganglia of the 'tween-brain and mid-brain.

It is easy to convince oneself that the optic tract splits in the human brain into two roots. The lateral (anterior external) root runs towards the lateral geniculate body. The mesial (hinder internal) root runs towards the mesial (internal) geniculate body (figs. 10 and 11).

(1) Part of the **lateral root** (fig. 168, *l*) enters the lateral geniculate body, *Cgl*. Another part spreads over it, forming the stratum zonale.

In Man, and still more in apes, the **external geniculate body** is heart-shaped in horizontal section, the apex being directed forwards. So deeply is it split that in certain frontal sections it often happens that we see two separate pieces, while only the sections farther forwards show the segments united into one.

The structure of the corpus geniculatum laterale, *Cgl*, is so characteristic that it is always easy to recognise. It consists of layers of grey and white matter irregularly rolled in one another (fig. 149). The white strata are formed partly of fibres of the optic tract and partly of others, which pass from the corpus geniculatum to the cortex. The grey layers are of two kinds, some of them consisting of large round nerve-cells, others of small cells, closely agglomerated.

The arborescent systems of a number of optic fibres reach the cells of the corpus geniculatum, and the axis-cylinder processes usually pass back towards the optic radiations, of which I shall presently speak.

A considerable portion of the external root, however, does not enter the lateral geniculate body, but passes on to the optic thalamus, *Tho*, or to the anterior corpus quadrigeminum, *Qa*. Many bundles of fibres slip under the external geniculate body, so as to reach the back part of the thalamus, the pulvinar, helping to produce its radial striation. Other fibres extend farther forwards on the surface of the geniculate body, and take part in the formation of the white layer which covers the thalamus (stratum zonale thalami). Very little is known about the ending of these fibres. Some of them undoubtedly sink into the substance of the optic thalamus.

Lastly, fibres sweep over the geniculate body into the brachium anterius, *Bqa*, and so to the anterior quadrigeminal body of the same side, *Qa*, and spread at first over the surface of it. Thus it comes about that the external root of the tract is in connection with the optic thalamus, the external geniculate body, and the anterior corpus quadrigeminum. These three grey masses have this in common, viz., they all give fibres to the corona radiata. The fibres join the sagittal medullary tract of the occipital lobe *Ss* (fig. 19), which comes from the posterior third of the posterior limb of the internal capsule and runs to the cortex of the hinder portion of the great brain, *Co*.

From the corpus quadrigeminum anterius the fibres of the corona are carried to the sagittal medullary tract by the brachium anterius. The cortical ending of the optic tracts will be treated of later on.

(2) The **mesial root** of the optic tract is easily followed to the **mesial**



**geniculate body**, in which some of its fibres end. This is a grey oval body united below the surface with the thalamus. Nerve cells of medium size are scattered through it, fairly uniformly; they are somewhat more closely packed in its ventral portion than elsewhere. Another small portion of the fibres of the internal root goes over the mesial geniculate body to the anterior tubercle of the corpora quadrigemina; while still another set of fibres goes directly into the posterior tubercle, perhaps without interruption in the mesial geniculate body. Our acquaintance with both origin and end of these fibres is, however, still imperfect.

Between the mesial corpus geniculatum and the posterior corpus quadrigeminum a close connection is established by fibres which course from the latter, through the brachium, to the former. In the posterior brachium fibres extend towards the great brain attaining to its cortex. The bundle of fibres which passes from the mesial geniculate body to the hemisphere seems to belong to the central organs of hearing and to attain to the temporal lobe, for *Monakow* found atrophy of the mesial geniculate body after extirpation of this portion of the cortex.

In most mammals the pulvinar thalami is very feebly developed, and in some it is lacking altogether, at least, externally. In proportion as it declines the external geniculate body becomes relatively large. The mesial geniculate body, too, is usually larger than in Man; in the horse, for example, it presents a remarkably strong development.

*J. Stilling* describes as a third or middle superficial root those fibres which run between the two geniculate bodies to the anterior tubercles of the corpora quadrigemina.

The fibres which branch off to the crus cerebri in front of the geniculate bodies, might be designated a deep root. They remain for a short distance in the outermost part of the crus (*Wernicke*), and then join themselves to the sagittal medullary tract of the occipital lobe as a direct cortical root of the optic tract, *Rd* (direct hemispherical bundle of *Gudden*). Probably the direct cortical root contains fibres from both optic nerves. *J. Stilling* asserts that he has followed a portion of these fibres spinalwards in the crus as far as the crossing of the pyramids (radix descendens). *Darkschewitsch* says that this descending bundle receives its myelin-sheaths considerably earlier than the proper optic fibres, and is therefore to be distinguished from them.

In the tuber cinereum, and in the portion of the anterior perforated substance over which the optic tract extends, lie large yellow pigmented nerve-cells (the basal optic ganglion), first described by *J. Wagner*. Nerve-fibres characterised by their considerable calibre, probably take origin in these cells, and course backwards in the optic tract, *CM* (Meynert's commissure). In Man they are separated from the optic tract by a thin layer of grey matter. These fibres ultimately leave the vicinity of the tract and traverse in curves the pes pedunculi; that they end in the corpus subthalamicum or the globus pallidus, as has been asserted, is highly improbable.

In the tuberculum cinereum (above Meynert's commissure, which



is myelinated earlier than the optic tract) we see some fine fibres, which cross in the middle line and then radiate apart (see fig. 152). *Darkschewitsch* calls this crossing 'Forel's decussation in the tuber cinereum.' Its fibres take rise directly from the optic nerve, and degenerate with it.

A weak root of the optic nerve, the basal optic root, passes from the chiasm directly into the central grey matter of the third ventricle.

When both optic nerves degenerate, a large part of both optic tracts also comes to grief, as well as the lateral geniculate body, the anterior tubercle of the corpora quadrigemina, and the back of the thalamus (the pulvinar). Portions of the tract, however — namely, Meynert's and Gudden's commissures — remain intact; they have, as these experimenters proved, nothing to do with the optic nerve itself, for they play no direct part in the act of seeing. Since the mesial geniculate and posterior quadrigeminal bodies do not suffer, we must accept it for a fact that the fibres of the commissura inferior (Gudden's commissure) run in the inner root of the optic tract, although they are not the only fibres which it contains. Very little is definitely known with regard to these remaining elements of the inner root.

Gudden's tractus peduncularis transversus, *Tpt* (fig. 11), is a portion of the brain which atrophies after degeneration of the optic nerve or destruction of the eye on the opposite side. It begins in the anterior quadrigeminal body, passes obliquely across the crus cerebri, hooks round its mesial border, and pierces the brain substance in front of the exit of the oculomotor nerve. Very little is as yet known concerning its subsequent course; *Perlia* observed a small bundle of its fibres ascending to the oculomotor nucleus.

Finally, *Darkschewitsch* finds that after extirpation of one eyeball, a bundle atrophies which leaves the tract on the side opposite to that on which the operation has been performed in the neighbourhood of the lateral geniculate body, extends through the thalamus and the pedunculus conarii to the pineal body, and so having crossed over to the side of the operation again, is supposed to reach the oculomotor nucleus through the ventral portion of the posterior commissure. It possibly takes part in reflexes of the pupil.

After what has been said it will be understood that the lateral geniculate and anterior quadrigeminal bodies, as well as the thalamus (and, indeed, the ganglion-cells of the retina ought also to be included), constitute the primary centres of the optic nerves. Of these, the corpus geniculatum laterale alone can be regarded as a visual ganglion in the strict sense of the term (*Henschen*); it alone is of functional value in conveying impressions of light; while the fibres of the optic nerve which terminate elsewhere, though taking part in the complicated mechanism of vision, do not transmit impressions of light from the retina to the brain. These grey masses mediate between the optic nerves and the cerebral cortex; they also serve to bring together other parts of the brain—*e.g.*, the corpora quadrigemina connect the optic



nerves with the nuclei of the eye-muscle nerves. A direct connection between optic nerves and cerebral cortex is also found in the direct cortical root of the tract.

The fibres which course from the primary visual centres to the cortex turn to the back and constitute a considerable tract, the sagittal medullary layer of the occipital lobe (Gratiolet's optic radiations) lying at first only on the lateral side of the posterior horn, but afterwards extending round to the mesial side also. The fibres from the corpus geniculatum laterale occupy the most ventral part of the tract, forming a bundle scarcely 1 cm. thick at about the height of the mesial temporal convolution and fissure (*Henschen*). The tapetum divides the bundles of the optic radiations from the ventricle, and the fasciculus longitudinalis inferior bounds them on the outer side.

The parts of the cortex which are to be regarded as the terminals of the optic fibres, the cortical visual centres, *Co*, are already fairly well known. We understand in this definition the occipital lobes and, perhaps, a part of the parietal lobes. But in the narrower sense it can only be applied to a limited area, devoted to the reception of impressions of light. This is the cortex about the fissura calcarina; a region which is characterised by peculiarities of structure which I shall describe later. Here we must seek the centre for sensations of light and colour received by the temporal half of the homo-lateral retina and the nasal half of the contra-lateral. According to *Henschen*, the macula lutea is represented in the anterior part of this region and the periphery of the retina in the posterior part; though there is no sharp delimitation between the fields of the crossed and uncrossed fibres.

In cases of long-standing disease of the occipital lobe degenerative atrophic changes have repeatedly been found in the primary optic centres; and sometimes the atrophy can be followed farther in the tract on the same side and in both optic nerves. *Monakow* produced a similar degeneration by destruction of the occipital lobe in animals. His experiments have proved that the importance of the anterior quadrigeminal tubercle to the faculty of vision is enhanced as we descend the scale, and that the two other centres play a more important part in those animals in which 'psychic vision' is the dominant factor.

A thick fibre-tract, also sagittally directed and running outwards from the optic radiations, the fasciculus longitudinalis inferior, connects the cortical visual centre with the temporal lobe of the same side. Further, fibres pass from the cortex of the fissura calcarina, through the forceps major (bulbus cornu posterioris) to the splenium corporis callosi (*Déjerine*). These probably constitute a connection between the visual centre and the contra-lateral temporal lobe, and possibly between the two centres themselves.

I must again point out that the inferior commissure, the mesial geniculate body, and the posterior corpora quadrigemina, must not be counted among the central visual organs, as they preserve their integrity after the destruction of the optic nerves, as well as after lesions of the



cortical visual area. They should probably be included among the auditory centres.

Of the physiological meaning of Meynert's commissure we know nothing at present.

A few words concerning the minute structure of the corpus quadrigeminum remain to be written; but here again I must observe that much yet awaits explanation.

**The Anterior Corpora Quadrigemina.** — We have already called attention to the very distinct arch of medullated fibres which is seen in transverse sections sweeping through the anterior quadrigeminal bodies over the aqueduct (*cf.* figs. 148, 149). The central grey matter which surrounds the aqueduct is cut off fairly sharply from the region belonging to the anterior corpus quadrigeminum, which lies on its dorsal and lateral sides, reaching as far as the brachium posterius, *Brqp.*

Proceeding from without inwards we meet with—

(1) A thin peripheral layer of white fibres, which probably originates directly in the optic nerve (stratum zonale or superficial medullary layer). In many herbivorous mammals this layer is so thin that the corpora quadrigemina appear not white, as in Man, but grey, owing to the underlying grey matter showing through.

(2) A not very thick layer of grey substance, the nerve-cells contained in which are small and few (peripheral grey layer, *cappa cinerea*, stratum cinereum).

(3) Grey substance with small nerve-cells and numerous sagittally running fine nerve-fibres which originate in the brachium anterius (strato bianco-cinereo superficiale, *Tartuferi*). *Ganser* divides this layer into three, the outer and inner containing more fibres, the middle more grey matter. This region corresponds to the proper nucleus of the anterior tubercle, *Nqa*, but it is difficult to delimit it from the second layer.

(4) The fourth layer, which is sharply marked off from the central grey substance around the aqueduct (strato bianco-cinereo profondo, deep medullary layer, layer of the fillet), consists of grey substance with cells like those of the preceding layer, and nerve-fibres which become closer and closer the greater the depth from the surface (and the nearer they lie to the roof of the aqueduct), and run either radially or in arched curves. Only a few of the innermost fibres of this layer have any further relation to the corpora quadrigemina, but many of them belong to the cerebral root of the fifth, and are recognised by the occurrence amongst them of occasional large vesicular cells which cannot be confounded with the other cells of this region. Besides the arched fibres of the fifth nerve a bundle of tegmental fibres is also found in this place, which courses towards the middle line and enters the fountain-like tegmental decussation.

In the rabbit, according to *Darkschewitsch*, the fibres for the optic tract come from the anterior two-thirds of the anterior corpus quadrigeminum of the same side, and principally from the outer part of its surface, while its mesial side gives origin to the fibres for the cortex cerebri.



After destruction of the optic nerves, it is the third layer of the corpora quadrigemina which comes to grief. In the mole and bat it is imperfectly developed. We may, therefore, conclude that this layer stands in direct connection with the optic tract, while the inner, more deeply-lying, medullary part of this layer is connected with the occipital cortex by way of the internal capsule; these latter fibres also atrophy after destruction of the portion of the cortex just mentioned (*Ganser*).

Thus, we see that the superficial medullary layer of the corpora quadrigemina is composed of optic fibres, the middle division of the medulla of fibres which course through the anterior brachium to the optic radiations and the cortex of the occipital lobe, while the deep medullary layer is, for the most part, made up of fibres ascending to, or descending from, the tegment.

A certain radial striation is usually recognisable in the anterior quadrigeminal body on slight magnification. This is due to the entering vessels which take this direction, and also to numerous fibres which, as I have already mentioned, assume a radial course.

The optic fibres, after spreading over the surface of the corpora quadrigemina, send their exceedingly abundant end-ramifications down to the deep layers, where they attach themselves to the nerve-cells of the grey substance. The course of the axis-cylinder processes of the cells of the corpora is best studied in the large deep-lying cells. These give off nerve-fibres which extend radially to the central-cavity grey substance. Here they first turn ventralwards, and then curve under the posterior longitudinal bundle towards the middle line. At the point where they exchange the radial direction for the downward curve they frequently divide, giving off an arched ascending ramus. Many of these cross the Sylvian aqueduct to the corpora quadrigemina of the other side. In numerous and graceful descending curves they enter Meynert's fountain-like decussation of the tegment, and turn spinewards after reaching the contra-lateral tegmental region. In Man they are said to join the fibres of the posterior longitudinal bundle (*Held*) and to mediate, directly or by collaterals, between this region and the nuclei of the eye-muscles.

The great number of 'spider' cells, each very rich in processes, which lie in the region of the anterior corpora quadrigemina, and are supposed to give to it its relative firmness and hardness, must also be pointed out.

The anterior quadrigeminal body is certainly in connection with the following parts of the brain:—

- (1) Directly with the optic tract through the anterior brachium.
- (2) With the lateral geniculate body, and so indirectly with the optic tract.
- (3) With the cortex of the occipital lobe through the anterior brachium and the sagittal medullary layer.
- (4) With the spinal cord (posterior column) through the mesial fillet.
- (5) With the nuclei of the eye-muscle nerves.
- (6) With the end-nuclei of the nervus acusticus through the lateral fillet.



As an immediate boundary of this crossing above the aqueduct, in the anterior quadrigeminal area, is to be found the **posterior commissure**, which arches forwards round it. We have already found in this commissure (fig. 149, *Fcop*), a tegmental tract which passes to the thalamus of the opposite side, as well as the tract which extends to Darkschewitsch's nucleus (nucleus of the distal commissure). The former can be followed on the ventral and lateral side of the posterior longitudinal bundle, far down into the medulla oblongata (*Edinger*). It is particularly well seen in the lower vertebrates. The remaining more considerable mass of the posterior commissure is not properly understood. It seems as if fibres of the fillet, perhaps also fibres from the posterior longitudinal bundle and the brachium anterius, enter into this commissure, in which it is always necessary to distinguish, as *Darkschewitsch* does, a dorsal and a ventral part. In the former, fibres from the deep medullary layer of the corpus quadrigeminum are supposed to extend to the cortex of the opposite side.

The posterior commissure is well-marked in all vertebrate animals, and is among the first tracts to be invested with myelin. This applies especially to its ventral part.

In the **posterior tubercle** of the corpora quadrigemina (fig. 147), as in the anterior, a stratum zonale is recognised, under which lies (in Man) a biconvex grey body, the ganglion of the corpus quadrigeminum posterius. For a considerable distance the nucleus of the two sides are continuous with one another in the middle line above the aqueduct. They contain but few large nerve-cells and a great many small ones. Some of the cells have long axis-cylinder processes, rich in collaterals, and some are Golgi's cells. Ventrally and mesially they reach almost as far as the cerebral root of the trigeminus. Fibres extend, from the anterior and lateral portions of these nuclei, through the posterior brachium to the mesial geniculate body, and so establish relations with the cortex cerebri and the mesial root of the optic tract. Fibres from the lateral fillet are seen to enter the ventral and lateral portions of the nucleus. Above the aqueduct, in this region also, there is a decussation into which part of the lateral fillet enters; and it is possible that some commissural fibres run in it.

In most mammals the posterior corpora quadrigemina form an eminence visible from the outside. In herbivorous animals it is small in comparison with the strongly developed anterior corpora, which in them are grey externally. In carnivorous animals the anterior and posterior corpora, which are white externally, are about equal in size. In the lower vertebrates the posterior tubercle is reduced to an insignificant ganglion in the lobus opticus, and is seldom visible from the outside.

The connections of the posterior tubercle are far less clear than those of the anterior:—

- (1) An indirect connection with the inner root of the optic tract.
- (2) With the cortex cerebri. This, as well as (1), is effected by the brachium posterius and the mesial geniculate body.
- (3) With parts of the system lying spinewards (the auditory centres especially) *viâ* the lateral fillet.



*Ferrier* and *Turner* found degenerated fibres as far down as the lateral column of the cord after destruction of the posterior corpora quadrigemina.

Besides ascending (and occasionally descending) **degeneration of the optic nerve** consequent upon a direct interruption of conductivity, primary processes of atrophy, the exact meaning of which escapes us as yet, occur in it as an accompaniment of various forms of nervous disease, such as tabes dorsalis, creeping paralysis, and disseminated sclerosis. Atrophy may also be induced by an independent neuritic process, usually interstitial in character, in the optic nerve itself. Very instructive are the rare cases in which an uncrossed bundle runs completely isolated in the optic nerve.

**3. Oculo-motor Nerve, Common Nerve of the Eye-Muscles.**—The root-bundles of the nerve for the eye-muscles in general originate in several groups of nerve-cells, which lie to the dorsal side of the posterior longitudinal bundles, *NIII* (figs. 148–150, 154). The whole oculomotor nucleus extends about 5 or 6 mm. in a sagittal direction.

The oculomotor nerve contains fibres destined for several muscles differing widely among themselves and more or less independent of each other in function. It is, therefore, not surprising to find that these different bundles arise from separate nuclei of origin. A superficial examination of the area in which the nerve originates is sufficient to show that, as a matter of fact, we can distinguish groups of small cells and groups of cells, relatively large, which may all claim, with more or less justification, to be regarded as its cells of origin.

To the dorsal side of the posterior longitudinal bundle we see a group of large cells occupying the entire region of the anterior corpora quadrigemina. This is the **lateral nucleus** (nucleus posterior of Edinger, chief nucleus of Kölliker), and is rendered conspicuous in Weigert's preparations by its grey colour, due to the rich network of fine medullated fibres which it contains. It is sometimes divided into a medio-ventral (fig. 169, *v*) and a dorso-lateral part (*d*). Some cells from this group can be followed towards the middle line, others thrust themselves among the fasciculi of the posterior longitudinal bundle, while some are found even on its ventral side, *b* (Bernheimer's lateral cells). Distalwards, between the anterior and posterior corpora or thereabouts, the lateral nucleus is joined by the nucleus of the nervus trochlearis (fig. 154), often with a slight interruption. These nuclei are easily distinguished in a cross-section, the round trochlear nucleus being embedded in a slight concavity of the posterior longitudinal bundle, and sending out fibres laterally, while the oculomotor nucleus, which is more elongated, merely lies close upon the same bundle, and sends its fibres ventralwards.

A second group of large oculomotor cells constitutes the **mesial nucleus** (central nucleus), fig. 169, *m*. This is club-shaped or fusiform, and unpaired, and lies in the middle line, neither beginning so far back nor extending so far forwards (brainwards) as the lateral nucleus.

Further, we should notice a group of smaller cells which usually lie on either side of the middle line, and can be followed laterally for a vary-



ing distance, the Edinger-Westphal nucleus (fig. 169, *EW*). It is, however, by no means certain that this should be taken as belonging to the region of origin of the oculomotor nerve. The constant mesial portion (small-celled mesial nucleus) has also been treated as distinct from the inconstant lateral portion (small-celled lateral nucleus). The nucleus of Darkschewitsch (upper oculomotor nucleus, nucleus lateralis anterior, nucleus of the distal commissure), visible at the level of the Sylvian aqueduct,

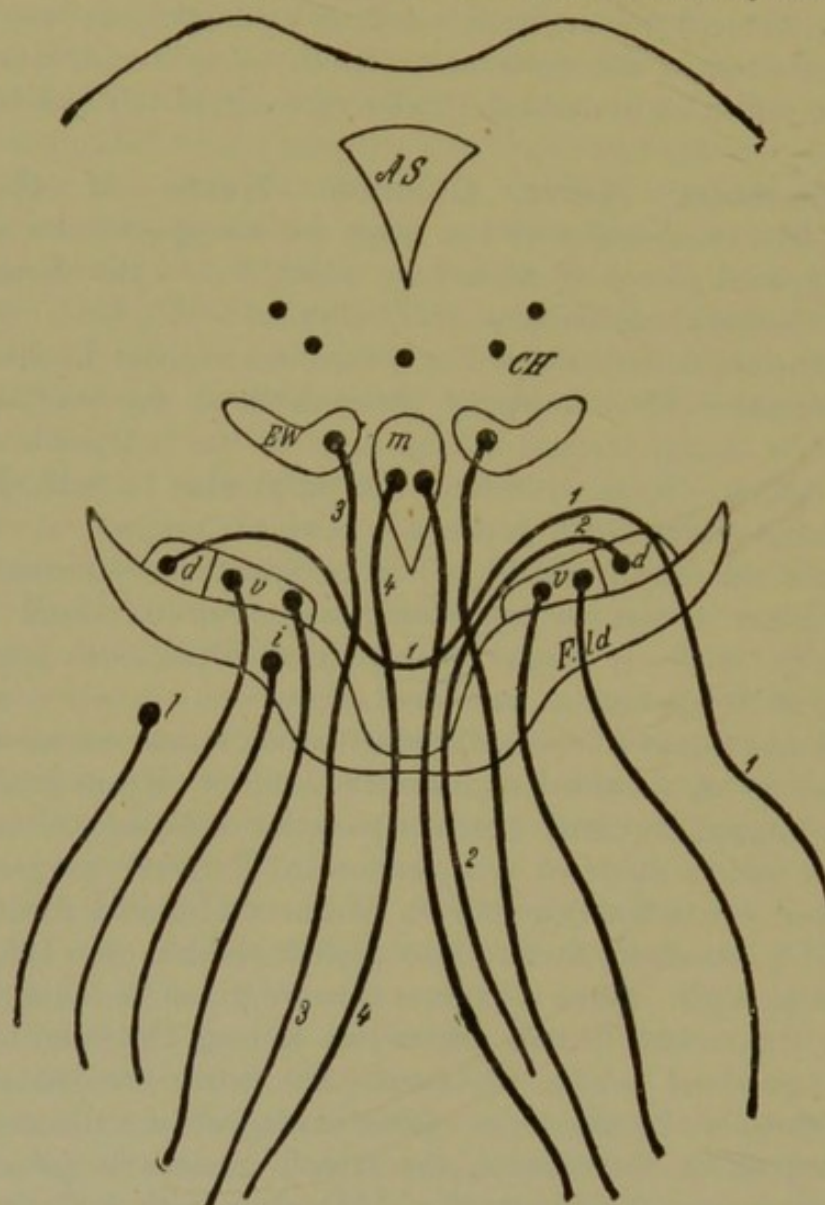


Fig. 169.—Scheme of the origin of the oculomotor nerve.—*v* and *d*, Ventral and dorsal portions of the lateral nucleus; *m*, central nucleus; *EW*, Edinger-Westphal nucleus; *i*, cells in the fasciculus longitudinalis superior (*Fld*); *l*, lateral cells; *CH*, central grey matter of the ventricle; *AS*, aqueductus Sylvii.

above the anterior part of the oculomotor nuclei just described and stretching considerably farther forward (as far, indeed, as to the wall of the third ventricle), has been regarded by some as a nucleus of origin of the oculomotor nerve, with which it has, however, certainly nothing to do. It belongs to the posterior commissure and the posterior longitudinal bundle (*cf.* p. 318).

Between these cell-groups and the aqueduct we find in the central grey



substance numerous large pale nerve-cells, often closely packed, with no intervening network of medullated fibres, such as is seen in the oculomotor nuclei. It is no less certain that these must not be looked upon as cells of origin for oculomotor fibres. *Siemerling* and *Westphal* erroneously held that the root of the trochlear nerve originates in this group.

It is, however, very probable that these cells stand in some relation to the oculomotor and trochlear nerves, though not in that of cells of origin.

The way in which the fibres of the oculomotor roots curve through the posterior longitudinal bundle, first into the region of the tegment, and then towards their point of exit, has been already described. In the most distal (posterior) sections in which root-bundles of the oculomotor nerve are still to be seen, they are usually found far to the side, leaving a large interval between themselves and the raphe.

The point of exit of most of the oculomotor fibres is to be looked for, as we know, in the trigonum interpedunculare, and especially in the sulcus oculomotorius. Not rarely single bundles traverse the crusta. This always happens in the case of the bundle which is sometimes present as an abnormal lateral root (p. 71). The root-fibres from the Edinger-Westphal nucleus (3) and the mesial nucleus (4) are very noticeably finer than those from the lateral nucleus, and are myelinated later (*Bernheimer*).

*Gudden* has proved that in the rabbit the origin of the oculomotor nerves is a half-crossed origin. In this animal the nucleus on each side is divided into two clumps, lying one above the other. The ventral group of cells belongs to the nerve of the same side, the dorsal group gives origin to fibres which cross to the opposite side. The ventral group lies a little farther forwards than the dorsal one.

More recent investigators have proved to demonstration that this partially crossed origin of the oculomotor nerve is common to many animals (the frog, rabbit, hen, and other mammals) and to Man. Crossed bundles (1) are found only in the distal part of the oculomotor region. They take rise from the dorso-lateral part of the lateral nucleus (*d*) and first pass ventralwards on its inner side. After crossing the middle line they ascend dorsalwards again, and pierce the posterior longitudinal bundle in such a manner as to form the most lateral of the root-bundles. The root-fibres (2) in the proximal part of the lateral nucleus also do not turn immediately towards their point of exit, but likewise run ventralwards on the inner side of the posterior longitudinal bundle, and then join the mesial root-bundles on the same side (*Cramer*).

This partial crossing of the root-fibres of the oculomotor nerve corresponds with the supposed double origin of almost all motor nerves (see the diagram, fig. 102, p. 199); and we know that most of the muscles supplied by it are governed from both sides of the brain. Whether direct commissural fibres mediate between the two oculomotor nuclei must be left an open question. *Nussbaum* believed that in the brains of cats he had discovered some fibres of this sort, and that they were most numerous in the spinal part of the region. These fibres myelinate early, but are probably simply the crossed root-fibres of the nerve.



*Duval* and *Laborde* believe that the oculomotor nerve of one side is connected, by means of the posterior longitudinal bundle, with the nucleus of the abducens nerve on the other side. The fibres, if they exist, take origin from the anterior pole of the abducens nucleus, sink somewhat ventrally in their course through the tegment, and, not far behind the oculomotor nucleus, go across to the opposite side in the dorsal tegmental decussation (*Nussbaum*). Here they meet with root-fibres of the oculomotor nerve, with which they join company, on the mesial side. This is an anatomical datum for explaining the harmonious working of the external rectus muscle of one side and the internal rectus of the other. If, however, we accept, with some slight modification, the view advanced by *Spitzka*, that the crossed oculomotor fibres serve mainly to supply the musculus rectus, there is no need for such a crossing as *Duval* and *Laborde* have described. A connection between the abducens and oculomotor nuclei would be enough to supply an anatomical datum for the synergism of the two muscles.

I may here remind my readers that numerous collaterals pass from the posterior longitudinal bundle to the nuclei of the eye-muscles. We are not yet sure of their origin and meaning.

*Hensen* and *Völkers'* experiments on the dog show that the individual terminal branches of the oculomotor nerve originate in different portions of the nucleus, which are arranged one behind the other sagittally, although, anatomically, they are imperfectly separated. Farthest brainwards lies, in the dog, the nucleus of origin for the nerves of accommodation, behind this the centres for the sphincter iridis, for the rectus internus, rectus superior, levator palpebræ, rectus inferior, and, last of all, for the obliquus inferior.

The most important and comprehensive experiments on this subject are those made by *Bernheimer* on apes. The external eye-muscles are supplied with nerves from the lateral nuclei in the following order: In the most posterior part, in front of the nucleus of the trochlearis, the nerve for the musculus rectus inferior of the other side originates; farther forward the nerve for the contra-lateral obliquus inferior, and perhaps for that of the same side; next the nerve for the rectus internus of the same side, and perhaps for that of the other; then follows the group for the rectus superior of the same side; and the most anterior portions belong to the levator palpebræ of the same side. The two-paired, small-celled nuclei (*Edinger-Westphal* nuclei), and the large-celled mesial nucleus must be looked upon as the nuclei for the internal muscles supplied by the oculomotor nerve.

[It is easy to trace the harmony between the arrangement of these nuclei in sequence from behind forwards, as described by *Hensen* and *Völkers*, and the several stages in the act of searching for an object and concentrating the gaze upon it. The head being first turned in the required direction, with adaptive movements of the oblique and other muscles of the eye, the object is searched for on the ground near the feet, whence the eyes



are directed outwards over the plain (superior recti), the lids being lifted from before the pupils. As soon as the object is found the eyeballs are converged upon it (by the internal recti), the size of the pupil is regulated to the amount of light (by the sphincter iridis), and, lastly, the lens is focussed for the distance. Although these several actions occur simultaneously as far as we can tell, it is clear that the position of the several nerve-centres coincides with the order in which the movements have been evolved.]

It appears that (in rabbits and guinea-pigs, at least) the fibres for the uppermost portion of the facial nerve, especially for the part supplying the orbicularis palpebrarum, originate in the most posterior (spinal) part of the oculomotor nucleus (*Mendel*) which stands in a peculiarly intimate functional relation to the act of seeing and the external eye-muscles. These fibres would then pass to the genu facialis in the posterior longitudinal bundle, and there join the other root-fibres of the facialis.

Small circumscribed foci of destruction, affecting only one cell-group of the oculomotor nucleus, are of extremely rare occurrence in Man.

The observations of *Kahler* and *Pick* that the pupillar fibres of the oculomotor nerve runs in its anterior bundles, are especially decisive. The posterior bundles of fibres are regarded as destined for the outer eye-muscles; they are divided into a lateral group (for the levator palpebræ, the most lateral, rectus superior, and obliquus inferior, which have a close functional connection), and a mesial group (for the rectus internus and rectus inferior).

The pupillar fibres and those of the nerves of accommodation run close to the middle line to reach their point of exit. They may therefore remain intact in diseases of the crusta which affect all the rest of the oculomotor region.

In several cases (*Leube, Spitzka*) ptosis has been observed in conjunction with the destruction of the most lateral part of the large-celled oculomotor group of the same side.

It must be allowed that the oculomotor nucleus is closely connected on the one side with the central mechanism of sight, and on the other side with motor regions of the cortex; our knowledge on these points is still, however, very imperfect. As coming within the former category must be mentioned the radial fibres which stream from the nuclei of the anterior quadrigeminal body into the central grey matter of the ventricle, and enter, farther on, into the fontanal decussation of the tegment. Possibly the numerous cells of the central grey matter may have some significance bearing upon the oculo-pupillar and other relations which exist between the nervous opticus and the nuclei of the eye-muscles. We know, moreover, that the arcuate fibres of the deepest layer of the corpora quadrigemina send numerous collaterals into the central grey matter of the ventricles (p. 345). According to *Bechterew's* view, which is not as yet supported by sufficient anatomical data, the centripetal fibres of the oculomotor nucleus which subserve pupillar movements are supposed not to extend backwards in the optic tract, but to leave at



the chiasm for the brain-substance, entering the central grey matter of the ventricle and extending to the oculomotor nucleus of the same side.

The tractus peduncularis transversus may also represent an indirect connection between the oculomotor nucleus and the optic nerve.

The connection between the oculomotor nucleus and the cortex cerebri may be looked for in all probability in the fibres which pass dorsalwards from the crusta to the raphe, cross one another at an acute angle, and form a fine network of nerves lying on the dorsal border of the lateral nucleus and the periphery of the central nucleus, but thickest in the nuclei themselves, into the substance of which the terminal fibres enter. It has not yet been settled from what part of the cortex cerebri these fibres pass in the corona radiata to the oculomotor nucleus. The same has to be said with regard to the relation of other eye-muscle nerves to the cortex. In some cases of cortical disease (especially of syphilitic origin) ptosis is the only symptom present as far as the eye-muscle nerves are concerned, so that it appears that the cerebral path of the fibres for the levator palpebræ, in its course towards the cortex, separates from the other eye-muscle tracts. The cortical centre for the levator palpebræ has been looked for in the gyrus angularis, since circumscribed disease of this part of the cortex is sometimes associated with paralysis of the opposite eyelid.

In the mole the nerves and nuclei of the eye-muscles are completely absent. In all other mammals the oculomotor nuclei are distinctly subdivided into a number of cell-groups, presenting, despite many variations in different species, a certain typical arrangement similar to that met with in Man. In birds two cell-groups can be distinguished, lying one above the other, while in reptiles the differentiation can hardly be recognised at all. It is most pronounced in Man (*Spitzka*).

**4. Trochlear Nerve (nervus patheticus, superior eye-muscle nerve).**—The origin of the trochlear nerve (anterior trochlear nucleus) is to be looked upon as the distal continuation of the nucleus of the oculomotor nerve (of the mesio-ventral portion of its lateral nucleus), from which it is not, as a rule, sharply defined. It lies on the dorsal side of the posterior longitudinal bundle and partly also in a groove in the same, *NIV* (figs. 147 and 154). Since the nucleus of the trochlear nerve lies in the plane of the front of the posterior quadrigeminal body, while it takes its exit from the brain much further back, at the front of the velum medullare anterius, it follows that its intra-cerebral course must be of considerable length (*cf.* fig. 146 in particular). Its course spinewards within the brain is somewhat complicated. The root-fibres which originate from the lateral and dorsal part of the nucleus slope outwards across the dorsal surface of the posterior longitudinal bundle (crus of origin, nuclear crus); they are then collected on the mesial side of the cerebral root of the trigeminal nerve into two or three round bundles, which bend spinewards and somewhat dorsally (the middle piece or descending crus), *IV* (fig. 146). When they reach the front of the velum medullare they lie close up against the dorsal edge of the cerebral trigeminal root; here they turn abruptly over towards the opposite side in the roof of the



aqueduct of Sylvius,  $IV^2$  (including the proximal angle of the fourth ventricle), and take their exit by the side of the brachium conjunctivum (crus of exit, root-crus),  $IV^3$ . As they curve round the proximal angle of the fourth ventricle they are almost the only things to be seen in the section (fig. 146  $IV^2$ ). Nothing in brain-anatomy is more certain than the crossing of the trochlear nerve in the velum medullare anterius; nevertheless, it is by no means impossible that a certain number of the fibres of the trochlear nerve take their exit with the issuing root of the same side. If this be the case the trochlear nerve is no exception to the rule with regard to the partial crossing of motor nerve-roots, although it would still be exceptional in the preponderance of its crossed root-bundles. *J. Stilling* describes fine roots which come out of the cerebellum, run brainwards through the lingula, and join themselves, perhaps without crossing, to the trochlearis. A rounded group of the most minute nerve-cells, which lies immediately to the spinal side of the proper (anterior) trochlear nucleus (*cf.* fig. 145, in which it is not lettered) was mistakenly considered by *Westphal* to belong to the trochlear nerve (*Westphal's* trochlear nucleus or posterior trochlear nucleus).

The numerous cells in the central grey matter of the third ventricle—called by *Westphal* and *Siemerling*, the chief nucleus of the trochlearis—to which I have already referred, have likewise no direct connection with the root-fibres of this nerve.

The fibres which pass in the root of the trochlear nerve towards the velum medullare do not all take rise directly from the nucleus, though most of the root-fibres start from its dorsal and lateral border, especially from the former (fig. 147). But as it courses above the dorsal border of the nucleus the bundle is joined by other fibres, which wind round the mesial border of the posterior longitudinal bundle and can be followed farther ventralwards. Some of them may, perhaps, cross the middle line and so constitute the crossed part of the trochlear root, but the majority certainly do not. The ultimate fate of these fibres is uncertain at present; possibly they pass laterally again in the posterior longitudinal bundle.

We may suppose that the connections of the trochlear nerve with the great brain (*viâ* the raphe), with the corpora quadrigemina anteriora, and with the posterior longitudinal bundle, is the same as that already described for the oculomotor nerve.

In the case of the trochlear nerve the intimate connection with the posterior longitudinal bundle can be verified. Fibres can be distinctly seen to emerge from among the cells of origin of the nerve and lose themselves in the thickened, club-shaped mesial part of the bundle. Nevertheless, *Nussbaum's* observations on kittens' brains can hardly be held to support the idea that there is a crossed relation between the root-fibres of the trochlearis and the abducens nucleus (as taught by *Duval* and *Laborde*).

When the intra-cerebral course of the trochlearis is studied in animals certain important differences, especially as regards its relations to the cerebral root of the fifth nerve, attract attention. In the monkey, in



which the nerve is comparatively well developed, we find the same conditions as in Man. In the cat and the dog its descending portion lies to the outer side of the cerebral root of the trigeminus. In the horse (and, perhaps, still more in the ox) it lies so close to the outer side of the root of the trigeminus that its bundles, as seen in transverse section, are disposed, not in a straight line, but in an arch convex mesially; the curve is due to its course medianwards towards the velum medullare. Its fasciculi pierce the trigeminal root and interlace with its fibres to such an extent that some of the easily-recognised cells of the trigeminal root get displaced into the bundles of the trochlearis. In lower animals (rodents) the interlacing in the trigeminal and trochlear roots is usually still more intimate. In all mammals, and also in birds, the decussation of the trochlearis can be easily demonstrated. In many mammals, the trochlear nucleus is quite embedded in the medullary substance of the posterior longitudinal bundle, sometimes, indeed, being shifted to the ventral side of it. In such cases, the issuing root-fibres in their passage lateralwards must constantly interlace with the longitudinal fibres of the bundle. The trochlear nucleus is said to be specially well developed in many reptiles, *Anolis* and *Iguana*, for example (*Spitzka*).

**5. Nervus Abducens (external eye-muscle nerve, nervus oculomotorius externus, sixth pair).—**The nerve to the external rectus muscle of the eye is only considered in this place on account of its relation to the other eye-muscle nerves.

We met with the nucleus of origin of the nervus abducens, *NVI* (erroneously called the facialis-abducens nucleus, upper facial nucleus, figs. 141 and 154), in the tegmental region, in the vicinity of the knee of the facial nerve. It appeared as a fairly well-defined, almost globular nucleus, its vertical axis only being somewhat extended, made up of large stellate cells.

From these cells the root-fibres of the abducens nerve originate, and leave the nucleus, for the most part, by its dorsal or mesial border. The former curl round it in close succession, turning first medianwards and then ventralwards, and unite with the fibres from its mesial border. They are thus collected into several root-bundles, which pass in gently curving arches ventralwards through the tegment and the most distal region of the pons to their point of exit. As this lies farther spinalwards than the nucleus, they must incline slightly in that direction. They appear to receive from the other side a very small accession of fibres, which pass beneath the ascending crus of the facial nerve, extend to the raphe, traverse it for some distance ventralwards, and enter the nucleus on its mesial border. In chickens' brains, *v. Gehuchten* further observed cells in the vicinity of the facial nucleus (the ventral abducens nucleus), from each of which a fibre proceeded first dorsalwards, then bent round and applied itself from the side to the abducens root. *Lugaro* also takes a similar accession for granted in the case of the root of the abducens.

Since the facial root, during a great part of its course, lies on the abducens nucleus, and fibres as a matter of fact seem to come out of the nucleus and apply themselves to the facial nerve, it is easy to make



pictures which give an illusory appearance of a partial origin of the facial nerve in this group of cells. *Gudden* and *Gowers* have, however, proved that the facial nerve has no connection with the grey mass in question, and that the fibres of the facial nerve which seem to come out of it really only cross it.

The abducens nucleus may be connected with the great brain by fibræ arcuatæ, which come down in the pyramidal tract, cross in the raphe, and pass into the abducens nucleus. We have already pointed out the connection between the abducens nucleus and the posterior longitudinal bundle (established principally by the collaterals of the latter), and the part which it, by this means, takes in the formation of the opposite oculomotor nerve.

A direct bundle of fibres goes to the abducens nucleus from the upper olive, *Ost* (stalk of the upper olive, fig. 172). In the brains of adults it is often hard to distinguish among the multitudinous fibres of all sorts, but it is very conspicuous in the brains of new-born animals, being already myelinated. Since the latter stands in close relation with the auditory nerve, it is possible that a nerve-root is thus provided by which reflex movement of the eyes in the direction of the sound may be effected. *Kölliker* thinks that a connection with the optic nerve may be established by the stalk of the olive, *viâ* the anterior corpora quadrigemina and the lateral fillet.

Its position in the knee of the facialis makes the recognition of the abducens nucleus easy in all mammals.

Disease of the nuclei of the eye-muscle nerves, which is, in many cases at least, analogous with poliomyelitis, is called poliencephalitis superior, or nuclear eye-muscle paralysis (ophthalmoplegia nuclearis).

A similar degeneration, affecting the motor nuclei farther spinalwards, and extending as far down as the hypoglossus nucleus, is known as poliencephalitis inferior, or bulbar paralysis. The two forms may be present in combination, and either may run an acute or a chronic course.

Acute poliencephalitis usually results from an encephalitic or acute hæmorrhagic process (poliencephalitis hæmorrhagica).

We may assume that in poliencephalitis superior, which is generally of a progressive nature, we have, as a rule, to do with a primary degeneration of the nerve-cells in the motor nuclei. The degeneration may vary in character, even in the same focus of disease, but always ends in atrophy. It is, however, not impossible that in many cases the primary disease is a hyperæmic and inflammatory process in the region of the nuclei, of which the degeneration of the nerve-cells is a secondary consequence.

Degeneration of single oculomotor nuclei, or circumscribed portions of nuclei, is frequently observed in tabes. Congenital wasting of the nucleus also occurs.

**6. Trigeminal Nerve (par quintum).—**If a line is drawn through the substance of the pons, inclining, from the point of exit and entrance of the trigeminal nerve, a little spinewards towards the angle which the floor and roof of the fourth ventricle make with one another, a region (fig. 143), called on this account the convolutio trigemini, is met with, in which the root-



fibres of the trigeminus converging from very various regions of the brain, come in contact with certain of its terminal nuclei or nuclei of origin.

It will be easier to impress upon the memory the several bundles which converge towards this point if we bear in mind that they come from four different directions, from the spinal cord and from the cerebrum,

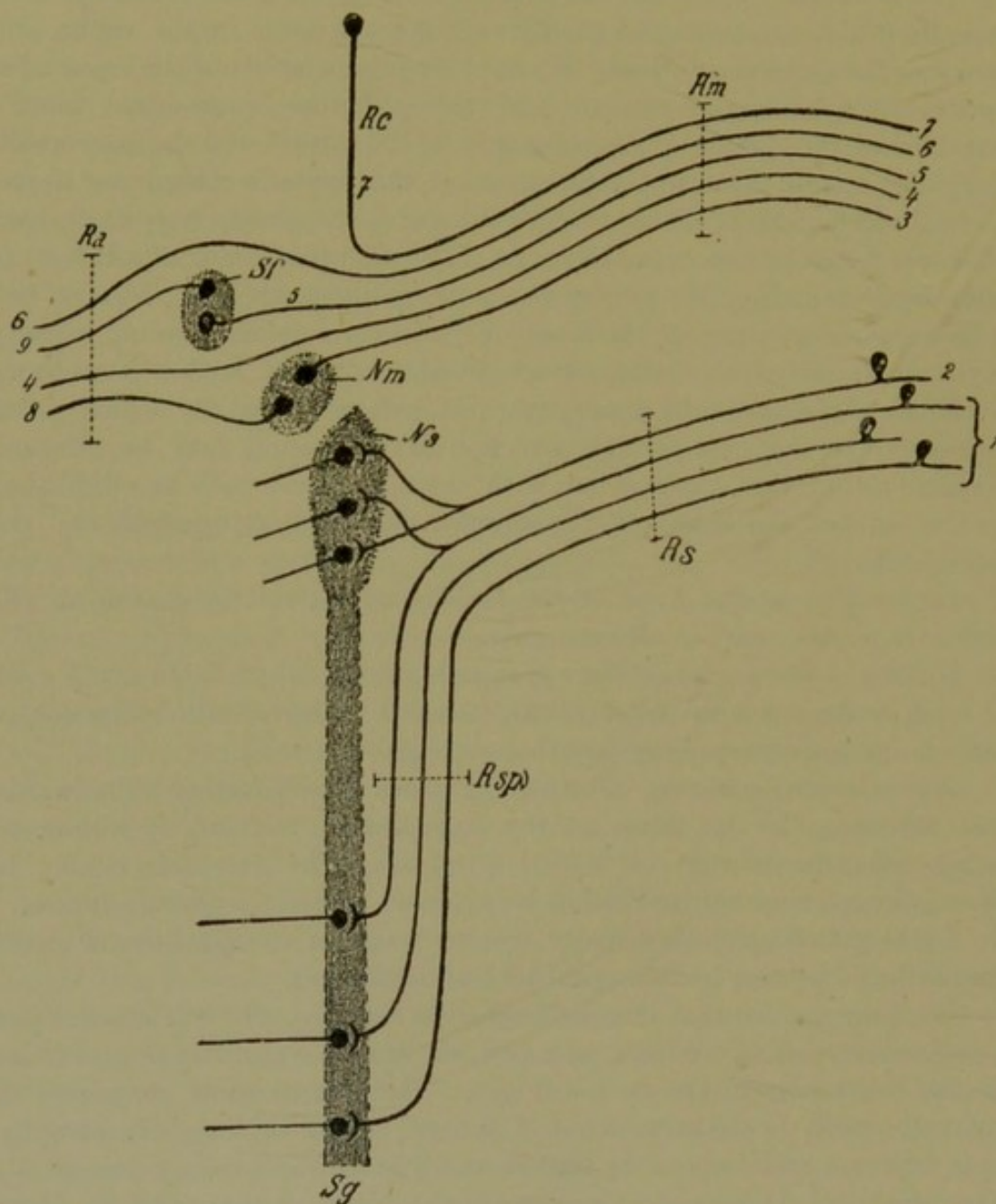


Fig. 170.—Scheme of the central origin of the nervus trigeminus.—*Rs*, Sensory root; *Rm*, motor root; *Rsp*, spinal root; *Rc*, cerebral root; *Ns*, sensory nucleus; *Sg*, substantia gelatinosa; *Nm*, motor root; *Sf*, substantia ferruginea; *Ra*, raphe.

from the side and from the middle line; and that they unite with other bundles which come from the sensory and motor nuclei of this region itself to form the two peripheral roots of the nerve (figs. 143 and 170, *Nm* and *Ns*; fig. 143, *NVm* and *NVs*).

The trigeminal nerve leaves the pons in two roots, the anterior, sensory,



much the larger (*portio major*), and the posterior, smaller, motor root (*portio minor*).

The point of exit and entrance from the pons lies somewhat in front of the region in which the converging roots collect (figs. 143 and 170). Hence the planes which we have chosen for our sections never show the trigeminal in its full extent as it traverses the pons. The sensory root, *Rs*, extends from the surface to the convolutio trigemini in a straight line directed spinalwards; the motor root, *Rm*, in an arch convex brainwards. The origin of the several separate root-fibres will now be traced.

**(a) Sensory root of the Trigemini (portio major).**

1. By far the most important of all the origins of the trigeminal can be followed as far downwards as the second cervical nerve. We have learnt to recognise the crescentic bundle which lies on the outer side of the substantia gelatinosa, increasing in size as the sections are carried farther forwards, and known as the **spinal root of the fifth** (in figs. 132 to 146 and in fig. 170, *Va*; in fig. 168, *Rsp*). This fibre-tract was formerly designated the radix ascendens, or ascending root of the trigemini; but since, physiologically, its fibres conduct downwards, and since, moreover, they nearly all take origin in the cells of the Gasserian ganglion, which lies outside the cord, and consequently course downwards, the name of descending root has lately been suggested for it. This name must, however, be avoided as likely to lead to confusion with the cerebral root, to which it was formerly applied and for which it must be retained; for this latter must on no account be called the ascending root. The best name for the bundle under discussion seems to be 'spinal root' (*racine bulbaire*). It constitutes the most important part of the sensory trigeminal nerve. The relation of the sensory trigeminal root to the Gasserian ganglion is the same as that of a posterior root to the spinal ganglion with which it is connected.

We may conclude that its mode of origin is similar to that with which we are already acquainted in the case of the posterior spinal roots.

The nerve-cells of the Gasserian ganglion possess a single process, which soon splits into two branches (*cf.* fig. 170), the one representing the peripheral nerve-fibre, the other the central root-fibre. As soon as the sensory trigeminal root has traversed the pons, most (or all?) of its fibres divide, like those of the posterior spinal roots, into an ascending and a descending branch. The ascending branch is usually much the finer, and often leaves the stem-fibre more after the manner of a collateral, and soon breaks up into its arborescent process either in the sensory trigeminal nucleus, which I shall presently describe, or in the substantia gelatinosa (*Ramón y Cajal*). The descending branches compose the well-known crescentic bundle of the spinal trigeminal root. Its lower end, blending by imperceptible degrees with the border zone of Lissauer, can be followed to below the decussation of the pyramids (*Bregmann*).

The fibres of the spinal root give off a large number of collaterals, some of which are said to have been followed into the (motor) nuclei of origin of the hypoglossus, facialis, and trigemini nerves (this is denied by *Ramón y Cajal*); and some into the substantia gelatinosa, in which they



break up (*Kölliker*). Numerous nerve-cells, large and small, have been pointed out in this region (especially by *Ramón y Cajal*). These would represent the terminal nucleus of the sensory trigeminal root. These cells are probably not confined to the substantia gelatinosa, but extend into the adjoining parts of the substantia reticularis.

After partial severance of the trigeminus we obtain a functional dissociation of the spinal trigeminal root. Whenever the fibres for the first branch of the trigeminus have been severed (in rabbits), degeneration has been observed in the ventral part of the crescentic cross-section. The fibres for the second and third branches occupy the dorsal division of this area (*Bregmann*).

Degeneration may, however, also be observed in scattered ascending (centrifugal?) fibres of the spinal trigeminal root (*Biedl*).

The cross-section of the spinal trigeminal root is traversed obliquely by the roots of the vagus and glossopharyngeal nerves.

2. The name of sensory trigeminal nucleus is given to closely packed clumps of grey substance consisting of small nerve-cells, distinguishable in carmine preparations, which are situate at the point where the spinal root turns towards the surface of the pons (*cf.* fig. 143). A great many sensory trigeminal root-fibres end in these cell-groups (middle sensory root, fig. 170, 2).

The sensory trigeminal nucleus extends a little farther brainwards than the entrance of the sensory roots, measures from 4 to 5 mm. in sagittal extension, and passes, on its spinal border, straight into the substantia gelatinosa. Histologically, however, it presents too many points of difference to be regarded as identical with the latter; at most it should be considered only as a modified form of this tissue.

3. From the region of the sensory trigeminal root we see fibres diverge laterally and stream into the cerebellum on the lateral side of the brachium conjunctivum (sensory cerebellar tract of *Edinger*; not represented in fig. 170). *Bechterew* and others deny this connection with the cerebellum, but are certainly mistaken in doing so.

Others, again, imagine a crossed ending for the fibres of this root. According to these writers, the bundles which will presently be described (under b, 2), belong, not to the motor root, but to the portio major, and merely pass through the distal part of the contra-lateral locus cœruleus, beyond which they can be followed farther lateralwards (*Poniatowsky*).\*

**(b) Motor root of the Trigeminus (portio minor, nervus masticatorius).**

1. The main body of the motor trigeminal root (3 to 7) originates in the motor nucleus (upper trigeminal nucleus, nucleus masticatorius) which can be

\* See the discussion of this question by the *translator* on p. 219. The formation known as substantia gelatinosa Rolandi lies on the concave side of the brush of fibres into which all sensory nerves spread out as they enter the cerebro-spinal axis. The substantia gelatinosa is hardly found in the mid-brain, for the nerves proper to this part are purely motor. Nor is it found in the 'tween-brain, for the two sensory nerves which belong to this region, the olfactory and optic, have their gelatinous substance placed peripherally in the olfactory bulb and retina respectively.



easily distinguished from the sensory nucleus. It lies on the mesial side of the sensory root, and consists of a single round grey mass of large multipolar cells. Its sagittal extension is considerably less than that of the sensory nucleus. Here originates the principal part of the motor root. We may look upon it as the proximal end of that part of the anterior horn (including the lateral horn) which was separated from the central grey mass by the crossing of the pyramids (fig. 171). It thus represents, to a certain extent, the continuation of the facialis nucleus.

[For morphological purposes it is somewhat important to distinguish between these horns, or rather columns of cells; the nucleus of the fifth, like the nuclei of the seventh and eleventh, belongs to the lateral column, which gives origin to nerves supplying the muscles derived from the 'lateral plates.']

A much smaller proportion of the root-fibres (4 to 8) turn towards the middle line in an arch slightly convex dorsally, cross the raphe not far below the floor of the ventricle, and proceed with but little change of direction to the motor roots on the other side.

This part of the crossed motor root of the trigeminus takes origin from the mesial part of the nucleus, which, in the early stages of development, is clearly distinct from the lateral part (*His*).

In electric fishes the motor nucleus is so much enlarged as to form an independent lobe of the brain.

2. The so-called crossed descending root of *Meynert* (6 and 9). It is highly probable that the nerve receives an accession of fibres from the large darkly-pigmented cells of the locus cœruleus (substantia ferruginea, *Sf*), by means of a bundle which runs from this group of cells close beneath the floor of the ventricle medianwards to the raphe, and after crossing and piercing the posterior longitudinal bundle, turns a little spinewards to join the sensory trigeminal root. The cells of the substantia ferruginea (fig. 144, *Lcö*) belong to the larger varieties (50 to 60  $\mu$ ) and are globular in shape; they contain a dark brown pigment in varying quantities, some having very little, while others are almost completely filled with fine dark granules. Some isolated cells of the substantia ferruginea are to be found deep in the substance of the tegment, and others in the roof of the ventricle.

A considerable number of root-fibres from the substantia ferruginea (5) apply themselves to the cerebral root (of which I shall speak presently), and pass with it into the motor root of the same side.

This connection between the trigeminus and the substantia ferruginea is denied by many (*Poniatowsky*).

The cells of the substantia ferruginea appear to be void of pigment in all mammals except Man.

3. From the region of the mid-brain the trigeminus receives an important accession, consisting entirely of thick uncrossed fibres which constitute the cerebral root (descending or anterior root, trophic root of *Merkel*), (figs. 143, 146; 171, *Vd*, and 170, ?).

The large round vesicular cells (45 to 60  $\mu$  in diameter), in which the



fibres of the descending root originate, do not form a compact group, but are either separate or united into little clumps which lie on the edge of the central grey matter, and may be followed as far as the plane of the anterior quadrigeminal bodies. In size and shape they closely resemble the cells of the substantia ferruginea, which latter show every transition, so far as pigmentation is concerned, to the neighbouring non-pigmented cells of the cerebral root, with which some of them mingle.

To the question whether these cells possess protoplasmic processes also, different answers have been given. If any such there be, they are very difficult to exhibit by the silver method; the axis-cylinder process is soonest stained, and they have consequently been called unipolar. *Ramón y Cajal* is of opinion that dendrites can be distinguished in the embryo, and that they afterwards fall victims to a retrogressive process. In successful carmine preparations, however, one can make sure that many (perhaps all) of these cells have several processes, some of which must be dendrites (*Kölliker* also holds this view). In the brains of young trout *v. Gehuchten* was able to demonstrate that the cells in question either possess a protoplasm process starting from them directly, or are unipolar at first, and then give off dendrites from their one process at some distance from the actual cell.

The cross-section of the cerebral trigeminal root forms a long figure, slightly convex outwards in Man, but in other animals usually straight (*cf.* p. 353). It lies up against the posterior longitudinal bundle and the cells of the substantia ferruginea. The other cells we have just been describing lie against the mesial border.

The further we advance forwards the smaller is the number of fibres which appear in the root in cross-section. When the anterior corpora quadrigemina are reached the few remaining cells of origin shift more and more to a dorso-mesial position, so that the uppermost fibres of the trigeminus curve downwards from somewhere near the middle line, as is shown by the occurrence of one or more of the characteristic vesicular cells above the aqueduct. The last of the trigeminal cells are sometimes found completely isolated at the level of the posterior commissure.

In the region of the substantia ferruginea the fairly thick nerve-fibres of the cerebral trigeminal root turn towards those which originate from the nucleus masticatorius, and the crossed motor fibres enter at the angle formed by the junction of these two strong bundles. The fibres of the cerebral root are said to send numerous collaterals into the nucleus masticatorius as they pass, which terminate in exceedingly rich plexuses (*Lugaro, Ramón y Cajal*).

*Merkel* ascribes trophic, *Huguenin* vaso-motor functions to the cerebral root; and certainly the cells of origin of these fibres differ so essentially in minute structure from the cells of the motor nucleus that they must also differ in function. This root has certainly nothing to do with the trochlearis, as *Golgi* supposes.

The **sensory root**, then, is composed of the following constituents:—

- (1.) The spinal root.



- (2.) The middle root from the trigeminal nucleus.
- (3.) The cerebellar root.
- (4.) The crossed sensory root.

The first and second are certainly constituents of the root, and are occasionally classed together as of equal value; the third is not accepted on all hands; and the fourth is somewhat uncertain.

The **motor root** is formed of fibres from—

- (1.) The middle root, which originates in the nucleus masticatorius; (*a*) chiefly uncrossed; (*b*) partly crossed.
- (2.) The substantia ferruginea; (*a*) crossed, (*b*) uncrossed.
- (3.) The cerebral root, uncrossed.

1*a* is certain, 1*b* very probable; 2*a* and 2*b* also very probable; 3 is certain.

The **connections of the trigeminal nuclei with the higher brain** must be complicated in proportion to the width of distribution of the nerve and the intricacy of its primary connections.

With regard to the main body of the sensory trigeminal tract, we may assume that the nerve-cells of the substantia gelatinosa and the sensory nucleus, among which the root-fibres terminate, send axis-cylinder processes medianwards. They thus form internal arcuate fibres (*Kölliker*), of which some remain on the same side (*Ramón y Cajal*), but the majority cross after traversing the raphe, and proceed through the tegment to the cerebrum (central sensory tract) as sensory fibres of the second class. They are said to give off numerous collaterals during their course, most of which pass to the nuclei of the motor trigeminus, the vago-glossopharyngeus, and the facialis nerves. I have already mentioned that the sensory root-fibres themselves, which are neurons of the first class, form connections through their collaterals with the motor nuclei of origin.

According to *Wallenberg*, the secondary trigeminal tracts of the spinal root do not originate from the substantia gelatinosa itself, but from the cells of the caput cornu posterioris situate at the mesial side of it. They cross somewhere in the vicinity of the hypoglossal nucleus, and subsequently lie on both sides of the hypoglossal roots and of the root of the facialis. Farther up, in the central grey matter of the ventricle, they lie on the outer side of the cerebral root of the fifth nerve, and finally stream into the thalamus with the mesial fillet. *Romanow* maintains that the fibres of the central tract of the motor portion of the trigeminus cross near the posterior corpora quadrigemina. They can be followed, however, to the motor trigeminal root of the same side as well.

It is most likely that the central motor tract detaches itself from the pyramidal tract and is formed by fibres which pass through the tegment (the most dorsal part of it, perhaps) to the raphe, and across it to the motor nuclei of the opposite side; but at present this has not been proved to a certainty. Similar fibres may pass to the cells of the substantia ferruginea and the cerebral root.

The cortical area for the muscles which the trigeminal nerve innervates occupies, apparently, the lower third of the anterior central and the neigh-



bouring portions of the middle and inferior frontal convolutions. A one-sided lesion of the cortex, especially when on the left side, paralyses the jaw-muscles on both sides (*Hirt*).

In most animals the trigeminus and the area in the central system from which it originates are far more strongly developed than in Man.

More or less extensive degeneration of the spinal root of the trigeminus is one of the most frequent concomitants of tabes, and may be present on either side or on both. It has also been observed in a case of chronic progressive poliomyelitis (*Böttiger*). It may lead to atrophy of the sensory nucleus of the nerve (*Oppenheim*). Degeneration of the cerebral root is very rare. In progressive bulbar paralysis and the bulbar form of amyotrophic lateral sclerosis the degeneration may extend to the motor nucleus; but as this constitutes the upper end of a continuous column of motor cell-groups (*cf.* fig. 171), there are very few cases in which the disease can advance so far brainwards without previously endangering the life of the patient.

**7. Facial Nerve (*nervus communicans faciei, portio dura partis septimi*).**—The nucleus of origin of the facial nerve lies very close to the spot at which the nerve takes its exit from the brain, but notwithstanding this the root-fibres have an extremely round-about course within the substance of the brain. Several times they turn in the wrong direction, and quickly leave it again before they have the good fortune to discover, after many wanderings, a way out of their prison. The way is made as narrow as possible owing to the pressing together of various structures.

Only a single nucleus of origin of the facial nerve is known with certainty (anterior or inferior nucleus), *NVII* (figs. 139 to 141, 154, and 171). It first appears in the most distal part of the pontal region, and extends some 4 mm. farther forwards. It lies in the *formatio reticularis*, on the mesial side of the ascending trigeminal root, nearer to the trapezoid fibres than to the ventricular surface. This nucleus is very characteristic, and is not easily confused with other structures, such as the upper olive.

Large lightly-pigmented nerve-cells lie in a ground-substance, which stains darkly with carmine, and is broken up into little bits by irregularly-disposed medullated fibres (root-fibres of the facial). We must look upon this nucleus as a thickening of the grey substance in the *formatio reticularis lateralis*, and thus also as a continuation of the separated portion of the anterior horn [? lateral horn] and the nucleus ambiguus. It is continued forwards by the motor nucleus of the fifth, although the two nuclei are not actually contiguous; spinewards its connection with the grey columns of the cord is kept up by means of the motor glossopharyngeal and vagus nuclei. The root-fibres come off from the nucleus either singly or in quite thin bundles. They converge in easy curves with a slight anterior deflection towards the part of the floor of the fourth ventricle, which lies on the dorsal side of the posterior longitudinal bundle (*VIIa*). This portion of their course is termed the nuclear crus of the facial nerve (crus of origin or ascending facial root).

Close to the middle line, on the dorsal side of the posterior longitudinal



bundle, which is thus pushed away from the ependyma of the ventricle, the facial fibres (by this time united into a single compact bundle, oval in cross-section), assume a directly sagittal direction, and course forwards on either side the sulcus longitudinalis, distinctly lifting up the floor of the ventricle (*eminentia teres*) for about 5 mm., *VIIb* (figs. 141, 142, 154, and 171). This intermediate portion of the root of the facial at first grows in cross-section, owing to the accession of fibres from the facial nucleus. It is known as the intervening or middle portion (the ascending limb, *fasciculus teres*, *Stilling's* constant root of the trigeminus).

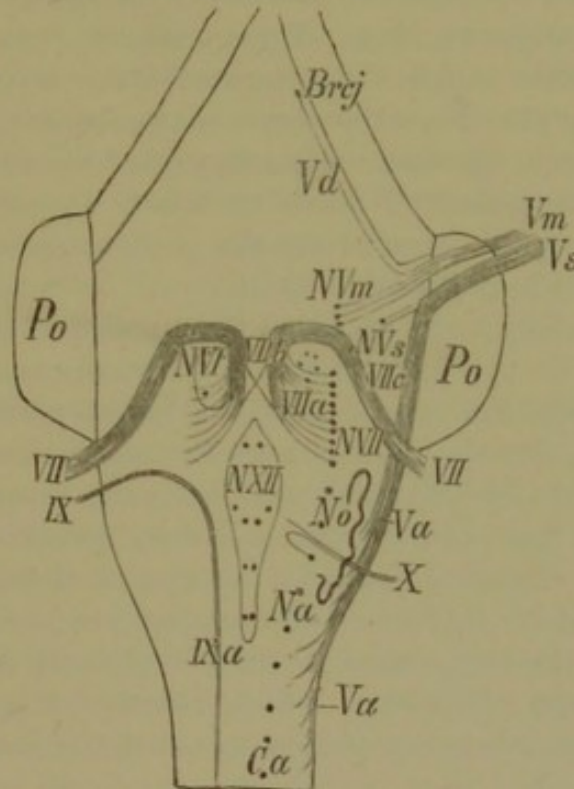


Fig. 171.—Schematic projection of the medulla oblongata.—*Po*, Pons; *Brcj*, brachium conjunctivum; *Va*, ascending, *Vd*, descending, *Vm*, motor, *Vs*, sensory trigeminal roots; *NVm*, motor, *NVs*, sensory trigeminal nucleus; *NVII*, facial nucleus; *VIIa, b, c*, facial root; *VII*, point of exit of facial nerve; *NVI*, nucleus of abducens; *IXa*, ascending glossopharyngeal root; *IX*, its point of exit; *No*, nucleus olivaris; *X*, vagus (or glossopharyngeal) nerve, with the origin of certain fine fibres in the nucleus ambiguus, *Na*; *Ca*, anterior horn of the spinal cord; *Ca, Na, NVII, NVm*, column of motor nuclei; *NXII*, nucleus of hypoglossal nerve.

Suddenly the facial root leaves the course just described at a right angle (fig. 142), arches a short distance beneath the ependyma dorsally to the abducens nucleus, curls down its outer side into the tegmental region (fig. 141), and runs towards its point of exit almost in a straight line ventrally, laterally, and distally, *VIIc* (issuing limb or root—fig. 140).

The double bending of the facial nerve is termed *genu nervi facialis*.

It is possible (fig. 141) to see in a single section the facial nucleus with its crus, the issuing limb on the outer side of the nucleus, together with the intermediate segment; and yet the three pieces of the root may appear to be in no way connected with one another.

In the intermediate segment the fibres are united in a single bundle; in



the issuing limb they are divided into separate bundles, lying close together and varying in number from four to eight.

Certain additions must still be made to what has been already said.

Fibres extend from the facial nucleus across the middle line to reach the root of the opposite side. Probably they form part of the beautifully-curved bundle which advances towards the raphe, between the posterior longitudinal bundle and the intermediate portion of the root (figs. 141, 142, and 154). The existence of this crossed root of the facialis has sometimes been called in question, especially by *Bregmann* and *v. Gehuchten*, as the result of observations upon degenerated nerves in rabbits, and by *C. Mayer* from similar observations on Man. These observers were never (or only in solitary instances) able to follow degenerated fibres across the middle line in disease of this nerve. From this circumstance *Lugaro* concludes that the fibres which come from the raphe only run part of the way with the facialis root, and then turn aside and leave it before its exit. Against these partially-explained results we must set the positive assertions of the most recent observers (*Cramer*, *Ramón y Cajal*).

We are bound to take for granted that fibres pass through the raphe to the facial nucleus from the pyramidal tract and the contra-lateral hemisphere of the great brain (with the exception of the lowest portion of the anterior central convolution, *Ecner*). Such a connection may be looked for, according to *Kölliker*, in fibres which come out from the ventral border of the pyramids and turn first medianwards and then dorsalwards to the raphe, and, after crossing, extend to the facial nucleus as the most ventral of the *fibræ arcuatæ internæ*. Fibres are also supposed to join themselves to the issuing limb from the cells which lie near it (*Laura*) as well as from the spinal trigeminal root (*Edinger*). I have already drawn attention to the important connections between the nuclei of the trigeminus and facialis (p. 361).

Since the upper branches of the facial nerve, which contain fibres for the orbicularis oculi and frontalis muscles, are not (as a rule) affected in central disease of the facial nerve so long as the root remains intact, wherever the seat of the disease may be, a different source in the brain has been sought for them. For this purpose the abducens nucleus was hit upon, as we have already mentioned; but this 'upper facial nucleus' or 'nucleus abducens et facialis' has, as a matter of fact, no connection with the facial nerve. According to *Mendel's* researches, if the muscles supplied by the upper facialis are destroyed (in a new-born rabbit), a conspicuous degeneration is perceptible after awhile in the posterior part of the oculomotor nucleus on the same side; it is therefore probable that the fibres intended for the superior facial originate in the oculomotor nucleus of the same side and pass to the genu facialis in the posterior longitudinal bundle, there to join the issuing limb. The circumstance that the most posterior part of the oculomotor nucleus remains sound after destruction of an oculomotor root accords with this theory.

The cortical centre for the upper facialis probably lies near that for the oculomotor nerve, perhaps in the inferior parietal lobe. At any rate, the fibres



which pass from the cortical centre to the oculomotor nuclei choose a course by which they avoid the parts of the brain substance in which apoplexies and similar forms of disease are most apt to occur. Only thus can the fact be explained that most of the muscles supplied by the oculomotor nerve, as well as those supplied by the upper facialis, often remain unaffected in disease of this character.

An interruption of the connection between the cortical centre and the nucleus of the facialis nerve, which is established through the knee of the internal capsule and the crusta, renders the voluntary innervation of the muscles which it supplies impossible, though both halves of the face may work under the influence of psychical emotion (laughter, pain, etc.) in the same manner as before (*Nothnagel*). In disease of the thalamus opticus, on the contrary, the voluntary innervation of both faciales may remain intact, while the contra-lateral half of the face shows no movement expressive of emotion. We may, therefore, conclude that the facialis nucleus is intimately connected with the thalamus opticus of the other side, probably through the tegment of the crus cerebri, and that these last-named tracts are devoted to the transference of reflex psychic impulses in the region of the facialis.

On the distal border of the pons another thin bundle comes to light between the apparent origin of the facial and auditory nerves, the nervus intermedius Wrisbergi (portio intermedia), also called the sensory root of the facialis. It can be followed at first towards the periphery with the other two, and afterwards unites with the facial nerve. It takes origin from the ganglion geniculi nervi facialis, which corresponds to the spinal ganglia in structure, and into which the chorda tympani enters as a peripheral nerve. The conditions met with in the central end of the nervus intermedius are probably to some extent similar to those found in the glossopharyngeus, and will be discussed in detail when we come to treat of that nerve.

In progressive bulbar paralysis and amyotrophic sclerosis the actual nucleus of the facialis is often drawn into the degeneration, while the part of the oculomotor nucleus which should be designated the superior nucleus of the facialis appears to remain intact.

In animals the intervening segment is so short that it is reduced to an arch uniting the nuclear crus with the issuing crus, and containing the abducens nucleus in its concavity (horse-shoe root of the facialis). In many animals (ruminant, for example, and ungulates with undivided hoof) the facial nerve is strongly developed and the nucleus is conspicuously large. It produces a distinct eminence, the tuberculum faciale externum, on the lateral surface of the medulla oblongata, behind the corpus trapezoides. This has been repeatedly mistaken for the superior olive.

In many animals the facial nucleus is distinctly divided into a number of separate groups. In the rabbit *v. Gehuchten* distinguishes three ventral groups of origin and one dorsal group. The cells of all bear the characteristics of motor cells.

**8. Auditory Nerve (nervus acusticus, portio mollis partis septimi).**—An inconvenience which is very commonly encountered in



treating of the anatomy of the central nervous system makes itself felt in a peculiar degree when we come to deal with the auditory nerve. I refer to the constantly changing designations of the particular nuclei from which the nerve takes origin, as well as of its roots. The cause of this confusion in nomenclature lies in the different meanings attached to terms expressive of relative positions (front, back, upper, under). I shall therefore restrict myself, as far as possible, to terms which do not lend themselves to misinterpretation.

It is satisfactory to note that we are coming to a clearer understanding of the course of the auditory tracts, and the divergent views of earlier days are beginning to give place to uniformity of opinion, at least on cardinal points.

The *nervus acusticus* of anatomists is composed of two distinct nerves, both conducting centripetally: (1) the *nervus cochlearis*, the actual auditory nerve; and (2) the *nervus vestibularis*.

Accordingly, we must distinguish **two roots** of the **auditory nerve**, which are easily kept apart in one's mind, owing to the fact that they lie on either side the corpus restiforme, *Crst.* All the fibres which reach the trunk of the auditory nerve on the outside of the restiform body constitute the lateral root, *Rl* (fig. 172). The fibres, on the other hand, which force their way through between the restiform body and the spinal root of the trigeminus, belong to the mesial root, *Rm.* If a series of sections is prepared, in the manner which has been advocated, it will be seen that the lateral root is found nearer to the spinal cord than the mesial root (it first appears in a section a little behind the one represented in fig. 139); while the mesial root is still seen in sections farther forwards than the lateral root extends (fig. 142). The names commonly used to distinguish the two roots are thus explained—the mesial root is also known as the 'deep,' 'superior,' or 'anterior' root; the lateral as the 'superficial,' 'inferior,' or 'posterior' root. It is generally understood that the lateral root belongs to the cochlear nerve, the mesial root to the vestibular nerve. The real auditory functions, therefore, belong to the lateral root, which might also be termed the *radix cochlearis*; while the mesial root (*radix vestibularis*) has other work to do, probably connected with the maintenance of equilibrium. The lateral root myelinates a little the later of the two.

#### (a) *Nervus cochlearis.*

The fibres which constitute the **lateral auditory root** originate in the ganglion spirale cochleæ. The cells of this ganglion are bipolar, like those of the spinal ganglia; their peripheral process penetrates into the organ of Corti, while the central process enters the stem of the root.

The **accessory auditory nucleus**, inclusive of the **tuberculum acusticum** (anterior, ventral, lateral nucleus of the anterior root, lateral acoustic nucleus, auditory ganglion), must be looked upon as the terminal nucleus of the lateral root; the portion of this nucleus which lies between the two roots of the nerve is known as the nucleus inferior, or lateral nucleus of the posterior root, *VIIIac* (figs. 139, 140, and 172, *Nac*).



This nucleus lies partly outside the proper brain substance on the nerve-stem. With the exception of the portion which is intercalated between the two roots, it lies within the lateral root and on its lateral side, and stretches up as far as the substance of the cerebellum. It is made up of small round cells closely packed together. At its proximal end the cells often exhibit a kind of capsule, reminding one of the arrangement found in the case of the spinal ganglia, though it must not be regarded as homologous with them. Again, it must be borne in mind as a possibility that the auditory fibres do not all join cells in the ganglion spirale, but that a number of them do not join cells till they reach the accessory acoustic nucleus.

A mass which is of no great size in Man, and is scarcely marked off distinctly from the accessory auditory nucleus, is known as the tuberculum acusticum, *Tba* (tuberculum laterale, superficial auditory nucleus, dorsal division of the acoustic ganglion). In most animals it is present as a longish body of considerable size, mounted, as it were, on the corpus restiforme just before it sinks into the cerebellum.

By Golgi's silver-method we can see that the auditory fibres which enter this nucleus first divide into two chief branches, and then subdivide freely, breaking up finally into extremely fine and rich terminal ramifications which surround its cells. They are reported to form a perfect basketwork of fibres and to end in club-shaped button-like swellings (*Held*). A small number of the auditory fibres do not end here, but pass into the striæ—presently to be described—or perhaps, into the corpus trapezoides (*Held*). The cells of the auditory nucleus proper have quite short processes, in this resembling the granules of the cortex cerebelli (fig. 60). Those of the tuberculum acusticum have, as a rule, two richly ramified dendrites, from the peripheral and central pole respectively, so that in a cross-section they usually appear to be placed radially.

The secondary sensory auditory tract takes rise in the accessory auditory nucleus and the tuberculum acusticum. At first it runs a double course, one part of it, the corpus trapezoides, passing medianwards ventrally to the corpus restiform and the spinal trigeminal root; and the other, divided into the striæ acusticæ, round the outer side of the corpus restiforme. From the cells of the auditory nucleus proper fibres go in either direction; from the tuberculum they nearly all pass to the striæ acusticæ.

The corpus trapezoides (or trapezoideum) consist for the most part of fairly fine bundles which can be followed in a slight curve to the upper olive, or beneath it to the raphe and so to the other side, piercing and splitting up the whole cross-section of the mesial fillet on their way. Groups of nerve-cells (the nucleus trapezoides) are scattered about through the substance of that part of the corpus trapezoides which lies between the upper olive and the root of the abducens. Here roundish cells are met with, the axis-cylinder processes of which go to augment the corpus trapezoides. Another conspicuous feature is the occurrence of thick axis-cylinders (observed in cats, dogs, rats, and rabbits, and known as *Held's* fibres) which extend to these cells and end among them in peculiar close fibre-baskets, cup-like swellings, etc. It is fair to say that *Kölliker* thinks



that most of these formations are artificially produced. These fibres come into connection with the nucleus trapezoides, but their subsequent course is at present unknown.

In most animals the corpus trapezoides is much larger than in Man, and lies exposed from the auditory nucleus down to the pyramids, on account of the much slighter spineward extension of the pons.

The fibres of the corpus trapezoides receive another accession from the *striae acusticae*, of which I shall presently speak.

With regard to the subsequent course of the fibres of the corpus trapezoides, we may say:—That some of them end in the superior olive of the same side; the majority in that of the opposite side; and some appear to join the lateral fillet.

The **superior olive** (small olive, nucleus olivaris superior, nucleus dentatus partis commissuralis, figs. 140, 141, 143, *Nos*; and fig. 158, *Os*) is insignificant in Man and many animals—*e.g.* the horse: in other animals (Carnivora, Rodentia, and especially Cetacea) it is well developed. It consists of a folded plate of grey substance and several indistinct subordinate grey masses lying to the dorsal side of the corpus trapezoides. The ground-substance of this structure scarcely stains at all with carmine. Its scattered round or fusiform nerve-cells (in the dog 40  $\mu$  in diameter) contain a yellow pigment, and are very closely packed together in some places. The terminal ramifications of the nerve-fibres which enter the superior olive are distinguished by their peculiar richness and fineness.

A small proportion of the fibres which take rise from the cells of the upper olive turn dorsalwards to the abducent nucleus (pedunculus olivæ superioris), but the majority unite with those from the lateral nucleus of the fillet to form the lateral fillet, the greater part of which ends in the posterior corpora quadrigemina, although a few of its fibres proceed farther to the anterior corpora (*cf.* p. 310). It is probable that a small part of the lateral fillet (auditory tract?) reaches to the commissure of the contralateral corpora quadrigemina posteriores.

The upper olive is also said to be connected with the roof nucleus of the cerebellum by the pedunculus cerebelli.

The name of ***striae acusticae*** (*striae medullares*) is given to fibres which come out of the accessory auditory nucleus and tuberculum acusticum, sling themselves round the corpus restiforme, and course towards the raphe under the floor of the fourth ventricle, usually so close beneath the ependyma as to be visible from the surface as a white line. Most of these fibres turn down ventrally towards the pyramids on the lateral surface of the raphe just before they reach the middle line, but they nearly all appear finally to cross over to the other side. Some of them arrive in this way at the region of the tegment, and there bend round in a longitudinal direction brainwards.

Another set of fibres of the *striae medullares* (*Kst*) cross one another in the most dorsal part of the raphe, and extend laterally and brainwards, to the vicinity of the locus cœruleus; their termination cannot be stated with certainty (*Popow* finds it in the brachium pontis); often these fibres



form a compact bundle (sometimes more than one) which lies beneath the ependyma of the ventricle, and is known as the conductor sonorus [in German 'Klangstab,' which Bergmann Latinised as above], fig. 12, *K*. Groups of middle-sized nerve-cells with several distinct processes are found here and there in the centre of the conductor sonorus, surrounded on all sides by its fibres (*Nussbaum*).

Some fibres enter the nucleus funiculi teretis, which reach it from the side in the tract of the striæ medullares.

The development of the white line visible from the surface varies enormously in different individuals. In animals the fibres of the striæ do not lie on the surface at all, but soon sink into the deeper parts.

At birth the striæ medullares are not myelinated.

Another set of fibres which serve as the central continuation of the accessory nucleus and tuberculum acusticum encircling the outer side of the corpus restiforme, scatter on reaching its mesial side, some of the diverging fibres of the bundle going to the large-celled nucleus, others to the triangular nucleus. Most probably they only traverse these nuclei on their way to the tegmental region, where they bend round brainwards and join the posterior longitudinal bundles. Some of these fibres, however, are supposed to pass downwards to the corpus trapezoides and to continue their course with it (*Kölliker's* dorsal bundle of the corpus trapezoides), so forming an indirect connection with the lateral fillet. But we must own that we are still in the dark as to the further course of most of the striæ medullares.

According to *Cramer*, fibres from the accessory nucleus pass into the pedunculus flocculi, and so enter the cerebellum.

Everything indicates that we have to look for the cortical centre of the sense of hearing in the temporal lobes, especially the gyrus temporalis superior and the gyri transversi, which take rise from it, and partly also in the gyrus medius. In favour of this localisation we have, apart from the results of experimental investigations, the appearance presented in cases of word-deafness, in which lesions of this region, especially on the left side, are almost always found. In the brains of deaf-mutes a very perceptible atrophy of the upper temporal convolution may be present, although the peripheral stem of the auditory nerve is intact.

*Monakow* has extirpated the temporal lobe in the rabbit, and found a consequent atrophy of the portion of the corona radiata which originates in it, and also of the corpus geniculatum mediale, associated in the case of the latter with an extreme degree of decay in the nerve-cells, loss of fibres in the brachium corporis quadrigemini posterioris, as well as atrophy of a portion of the zona reticulata of the optic thalamus. The same results can be shown in the human brain when defect of the gyrus temporalis superior has subsisted since infancy. Thereby an unbroken chain between the peripheral nerves of hearing and the cortical acoustic field is completed, its links being:—ganglion spirale; radix cochlearis; nucleus accessorius; corpus trapezoides; oliva superior; lemniscus lateralis; corpus quadrigeminum posterius; brachium corporis quadrigemini posterioris; ganglion



geniculatum mediale; (posterior part of the internal capsule?); lobus temporalis.

The investigations of *Ferrier* and *Turner*, however, lead us to conclude that a considerable proportion of the fibres of the corpus trapezoides pass without interruption straight into the corpus geniculatum mediale.

The last neuron of this chain is furnished by the cell in the ganglion geniculatum mediale, the nerve-fibre of which traverses the internal capsule and breaks up among the cells of the cortex of the temporal lobe. For the sake of simplicity, the fibre (*Qp Co*) in fig. 172 is drawn as if proceeding straight from the posterior corpus quadrigeminum to the cortex.

*Spitzka's* comparative observations also favour the existence of such an auditory path. In many cetacea he found an extremely marked development of the posterior auditory root, corpus trapezoides, posterior corpus quadrigeminum, and corpus geniculatum mediale.

We must not, however, forget that the nucleus accessorius, and with it the nervus cochlearis, must have other central connections; as, for example, through such fibres of the striæ acusticæ as do not intermingle with those of the corpus trapezoides, but can be followed farther brainwards in the cross-section of the tegment. Perhaps these constitute the connection with the thalamus opticus which must certainly exist.

*Held* took for granted that the nucleus accessorius and the cortex were connected by a direct cortical tract, but neither as the result of experiments on animals nor of disease in Man has degeneration been followed beyond the corpus geniculatum mediale, even when the loss of the convolutions in question has been congenital or of very long standing. The fillet, corpus trapezoides, and accessory auditory nucleus seem to remain absolutely intact, which excludes the possibility of a direct connection between the last-named and the cortex. Thus here we are face to face with conditions wholly different from what we have met with in the optic central organs, where the degeneration induced in young animals by removal of the visual sphere can be followed right down to the optic nerve.

The cortical sphere of the auditory nerve is connected with the ganglia of the pons by the temporal pontine tract. Moreover, the two spheres are brought into connection with one another by means of fibres which course in the forceps corporis callosi; and, finally, it has been proved that association-fibres pass hence to the gyrus angularis and the occipital lobe (*Ferrier* and *Turner*).

(*b.*) **Nervus Vestibularis.**—The fibres of the mesial root represent the central processes of the bipolar nerve-cells which compose the ganglion vestibulare (*Scarpa's* ganglion). The peripheral processes of these cells take rise in the wall of the membranous semicircular canals.

Lying at first close up against the mesial border of the accessory auditory nucleus, the thick bundle of the mesial root squeezes itself between the corpus restiforme and the spinal root of the trigeminus, and spreads out on the dorsal side of the latter towards the triangular and large-celled nuclei, the terminal nuclei of the vestibular nerves; every fibre (it is said) dividing fork-like on its way.



(a.) The **triangular nucleus** (*nucleus triangularis*, triangular auditory field, chief nucleus, central or inner nucleus, nucleus posterior, mesial nucleus of the posterior root, dorsal nucleus, mesial portion of the nucleus superior or nucleus dorsalis), *VIIIh* (figs. 139, 140). A symmetrical grey area is seen in the sections which show the most anterior points of exit of the hypoglossal nerve (fig. 137); it lies at first on the outer side of the chief nuclei of the glossopharyngeal and vagus nerves, but reaches to the raphe in sections farther forward, and assumes then a triangular form, its hypotenuse corresponding to the surface of the ventricle. Still farther brainwards it retreats again from the middle line. It disappears in the region of the abducens nucleus. It may therefore be called the triangular nucleus, a title which sufficiently describes it. Throughout the whole cross-section we find nerve-cells, large and small, not combined into distinct groups, but dispersed at rather wide intervals in a moderately close network of fibres. Soon after the hypoglossal nucleus has disappeared some fairly large fusiform cells come into view on the ventral border of the triangular nucleus, near the middle line. They are closely packed, with their axes transversely placed, and seem to have some connection with the conspicuous bundle of nerve-fibres which wraps round the ventral border of the nucleus and passes through the raphe, with a slight inclination ventralwards, into the substantia reticulata of the other side. It has not been proved, however, that these cells belong directly to the auditory nerve.

Isolated large nerve-cells are also to be found more laterally situate in the ventral parts of the auditory nucleus.

In consequence of its relative poverty in cells, and of the fact that the terminal ramifications of the nerve-fibres are not very rich, this nucleus looks fairly light in Weigert-preparations and after impregnation with silver.

A well-defined group of fusiform cells is constantly found in the mesial angle of this triangular field, where it attains to its greatest cross-section (*nucleus funiculi teretis seu medialis*). This group reaches beyond the limit of the nucleus, both on the cerebral and spinal sides, and has some uncertain direct connection with the auditory nerve, *Nft* (figs. 137-141). In many brains the nucleus funiculi teretis attains a remarkable size, and fibres can then be seen issuing from the nuclei on either side. These fibres unite in the middle line and form a bundle which courses brainwards beneath the ependyma, and may be called the mesial longitudinal bundle. It appears to find its terminus in the nucleus centralis superior.

(b.) The **large-celled nucleus**.—Under this name we include several groups, not clearly marked off from each other, which serve as termini for the fibres of the nervus vestibularis.

On the mesial side of the corpus restiforme, where it first comes into existence, a nearly rectangular area is met with, readily distinguishable from its surroundings, and consisting of nerve-bundles cut across and separated by very little intervening grey substance (figs. 137-141, *VIIIa*).



*Roller* has shown that these fibres take origin directly in the auditory nerve, and constitute, therefore, an ascending (or, more correctly speaking, a descending, or spinal) root. The farther we advance towards the proper acoustic region the more extensive does the whole space occupied by grey matter become, while the nucleus increases correspondingly. Especially in the most anterior sections (fig. 141), in which these fibres, then the main constituent of the mesial root, are bending laterally and ventrally towards the point of entrance of the nerve, numerous nerve-cells conspicuous for their size are scattered about. The distinctive name of *Deiters' nucleus* has been given to this region (lateral division of the dorsal nucleus, exterior auditory nucleus, mesial nucleus of the anterior root). It lies in the lateral part of the floor of the fourth ventricle, but changes its place as soon as the corpus restiforme streams into the cerebellum, and reaches the lateral wall of the ventricle. It is particularly well developed at this point, and is known as *Bechterew's nucleus* (nucleus angularis, chief nucleus of the vestibular nerve). In *Deiters' nucleus* the nerve-cells are remarkable for their size, as has been observed before, but it is in *Bechterew's nucleus* that they attain the largest dimensions. In most animals they are considerably larger than in Man. The dendrites of these cells are sometimes very long, and the nerve processes go off in every imaginable direction (*Sala*).

The large-celled nucleus consists, then, of—(1) the spinal auditory root; (2) *Deiters' nucleus*; (3) *Bechterew's nucleus*.

Many writers (*Sala* among them) maintain that root-fibres or ascending bifurcated branches (*Ramón y Cajal*) of the vestibular nerve pass straight into the cerebellum on the lateral side of the large-celled nucleus.

I would again lay stress upon the fact that the greater number of the vestibular fibres end in this nucleus, and only a small proportion in the nucleus triangularis.

With the exception of the connection with the cerebellum, very little is known of the connections and relations of the terminal nuclei of the vestibular nerve.

Strong and rather undulating bundles of nerve-fibres course dorsally to the cerebellum from *Deiters' and Bechterew's nuclei*, and are perhaps joined by fibres from the triangular nucleus. The auditory tract of the cerebellum lies on the mesial side of the pedunculus cerebelli, laterally to the brachium conjunctivum, into which a considerable number of its fibres enter. The remaining bundles ascend to the vermis, and end (usually after crossing) in the nuclei of the roof, and probably also in the nuclei emboliformis and globosus.

The following remarks may be offered on the subject of the parts of the brachium conjunctivum just mentioned. The more dorsally-lying localities in which the auditory nerve originates, *Bechterew's nuclei*, as we have called them, are, according to *Flechsig*, united with one another by commissural fibres which come out of the cerebellum in the brachia conjunctiva and bend round in arches in the posterior angle of their decussation. *Mendel* had already found that the auditory nerve sends a



considerable bundle to take part in the formation of the brachium conjunctivum. *Ramón y Cajal* gives the name "nucleus cerebello-acusticus" to a group of large nerve-cells attached to the central ganglia of the cerebellum (in the rat), in which lies the bundle which courses from the large-celled nucleus to the cerebellum. Contrary to the generally received opinion, he holds that all, or at any rate most of these fibres take origin in the cerebellum and end in the nuclei of Deiters and Bechterew.

Very little can be stated as certain concerning the cerebral connections of the nuclei of the vestibular nerve.

1. The Triangular Nucleus.—Out of the mesial angle of the triangle, plenty of fibres, not collected into bundles, extend through the posterior longitudinal bundle to the raphe (*Freud*) and the tegmental region (5). Probably they form, therefore, a central connection of this nucleus. Along the whole ventral border fairly numerous fibres, not collected into bundles, pass out ventralwards, and can be followed, like a fine shower, far into the substantia reticularis towards the cells of the nucleus lateralis medius.

2. The Large-celled Nucleus.—Strong fibres originate in the large-celled nucleus, and run in a ventro-mesial direction, crossing through the issuing limb of the facial nerve into the tegmental region, where they bend over and assume a longitudinal course (spinewards, perhaps, as well as brainwards) between the abducens and facialis nerves (1). Other thick fibres extend as arcuate fibres into the raphe (4) and the tegment of the opposite side; and, in this way, perhaps, reach the great brain (fig. 144).

Further, it is easy to discover fibres which course from Deiters' nucleus to the nucleus of the nervus abducens; and not a few of the fibres of the former are said to join the corpus trapezoides.

The relations between the nuclei of the vestibular nerve and the cortex cerebri seem to be of no great importance; which answers to the physiological fact that the impulses conducted through it seldom pass the threshold of consciousness. Its connection with the cerebellum, on the contrary, is, as we have seen, extremely intimate.

[The eighth nerve is a pure sensory nerve. It appears, however, to carry two distinct kinds of impressions. The organ of Corti is regarded as the organ for the analysis of sound. The cochlear nerve carries, we therefore suppose, the impulses generated by the impact of sound-vibrations of varying period. In the semicircular canals of the labyrinth originate impressions of orientation, while the hair-cells of the utricle and saccule may take cognisance of the amplitude of sound-vibrations. Such is the allocation of function commonly ascribed to the several parts of the internal ear, although in neither case can it be said to be placed beyond the reach of doubt.

Turning to the auditory nerve, this, as already pointed out, consists distinctly of two separate parts—(1) the ramus lateralis *seu* cochlearis, which is the first to myelinate (when the foetus is about 30 cm. in length); (2) the ramus medialis *seu* vestibularis, the fibres of which acquire their medullary sheaths somewhat later (when the foetus is about 38 cm. in length).



Despite this complexity in its functions the auditory nerve is, like the olfactory and optic, limited in its distribution to a single organ of a single segment; we may, therefore, expect to find that, unlike the multi-segmental fifth, ninth, and tenth nerves, it will have a defined connection with the central tube of grey matter within the cerebro-spinal axis. This is conspicuously the case, for the small-celled grey matter, which is the upward continuation of the posterior horn of the spinal cord, undergoes a great local development beneath the floor of the fourth ventricle. Into this grey matter the auditory nerve pours its impulses, and it is open to doubt

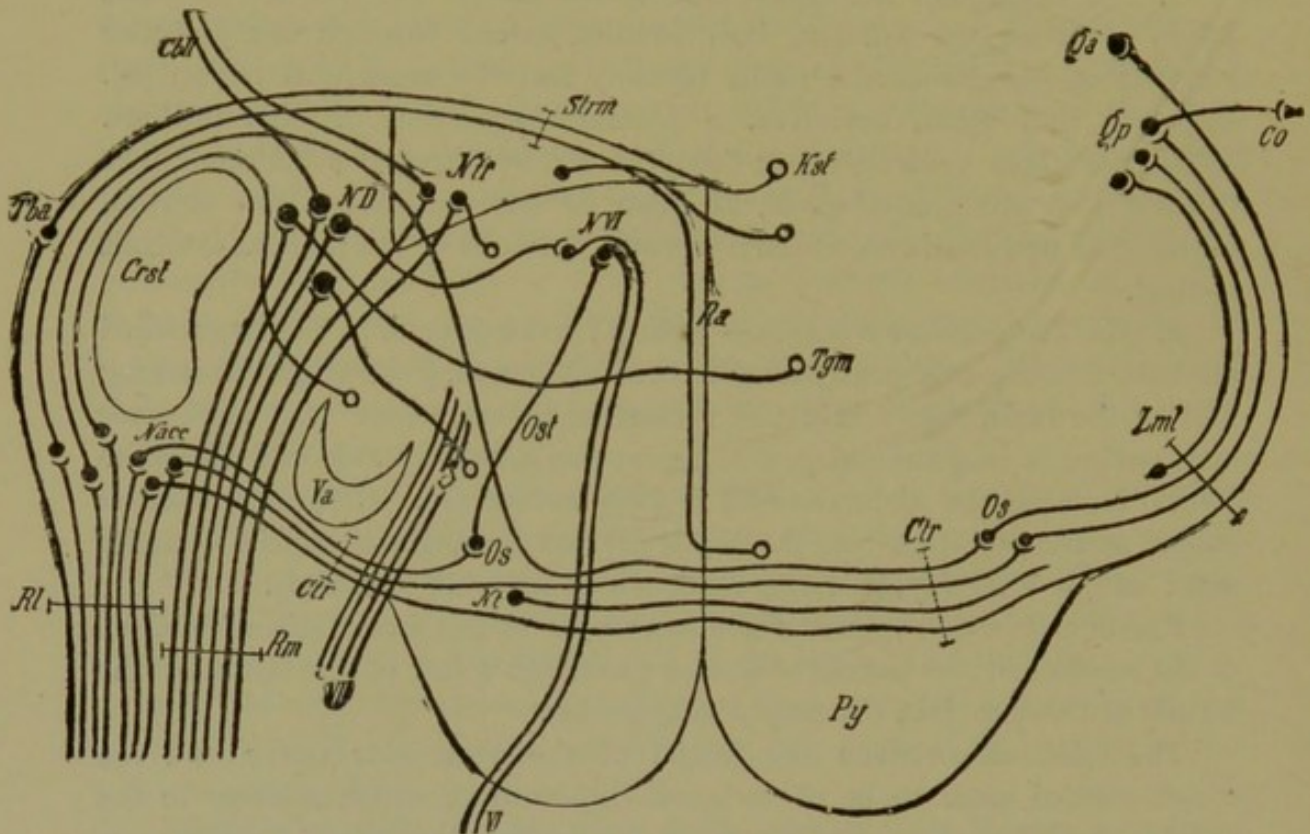


Fig. 172.—Scheme of the central auditory apparatus.—*Va*, Spinal trigeminal root; *VI*, root of the abducens; *VII*, root of the facialis; *Cbl*, cerebellum; *Co*, cortex cerebri; *Crst*, corpus restiforme; *Ctr*, corpus trapezoides; *Kst*, conductor sonorus; *Lml*, lateral fillet; *NVI*, nucleus of the abducens; *Nacc*, nucleus accessorius; *ND*, Deiters' nucleus; *Nt*, nucleus of the corpus trapezoides; *Ntr*, triangular nucleus; *Os*, superior olive; *Ost*, peduncle of the superior olive; *Py*, pyramids; *Qa*, *Qp*, anterior and posterior corpora quadrigemina; *Ra*, raphe; *Rl*, lateral auditory root; *Rm*, mesial auditory root; *Strm*, striae medullares; *Tba*, tuberculum acusticum; *Tgm*, tegmental region.

whether the search for other nuclei of the auditory nerve is likely to prove profitable. The accessory nucleus is probably a posterior root-ganglion. It hardly appears large enough to take the place of root-ganglion to the whole auditory nerve, nor is this by any means necessary, for just as we find bipolar cells on the fine filaments of commencing olfactory and optic nerves (in the olfactory bulb and retina respectively), so we find the cochlear nerve-fibres connected, before they leave the ear, with the bipolar cells of the ganglion spirale.

That sensory nerve-fibres join large multipolar cells appears unlikely to



many anatomists. The *translator* is inclined to look upon the so-called large-celled nucleus of the auditory as homologous with the scattered cells of the posterior horn, and to suppose that these cells collect filaments from the sensory plexus and despatch medullated fibres to the cerebellum and elsewhere. It does not appear that the nucleus of Deiters atrophies after destruction of the ear (*Baginsky*).

It is well to remember that while the primary connections of the auditory nerve are likely to be simple, its secondary connections must certainly be extremely complex, for not only do sensations from the ear play an important part in orientation, but auditory impulses start innumerable protective movements, and also take part in the highest degree in intellectual life.]

Neoplasms of various kinds originate in the nervus acusticus. According to *Virchow*, they are more frequent in this nerve than in any other. Chalky concretions have been repeatedly observed in the auditory stem. In a severe case of aural hallucination *Flehsig* found the posterior corpus quadrigeminum permeated with them.

**9. Glossopharyngeal Nerve.**—From the distal border of the pons spinewards we meet with a succession of nerve-roots, which at first come out through the side of the restiform body dorsally to the eminentia olivaris, and lower down in a line continuing spinewards in the same plane as far as the region of the sixth cervical nerve. These roots belong to the ninth, tenth, and eleventh pairs of cranial nerves.

Since the root-bundles of these nerves join one another it is impossible in the case of most of them to say, without preparation of their peripheral nerve-stems, to which of the three they belong, especially as their central origin also agrees in many points. The uppermost roots belong, without doubt, to the glossopharyngeal nerve; the lowest, especially when they come out from the spinal cord, to the spinal accessory.

In the glossopharyngeal nerve we must distinguish between sensory and motor root-fibres.

The sensory fibres end in various ways (fig. 138).

(1) The **dorsal vago-glossopharyngeal nucleus** (small-celled, sensory or posterior glossopharyngeal nucleus). A portion of the entering glossopharyngeal fibres can be seen, taking a fairly straight course medianwards, with a slight inclination dorsalwards, through the spinal trigeminal root to their terminal nucleus, a group of cells on the lateral side of the hypoglossal nucleus in the floor of the fourth ventricle. This group is almost destitute of the feltwork of fine medullated nerves, to which, in *Weigert's* preparations, the hypoglossal nucleus owes its pale grey colour, so that this region is easily distinguished by its brightness of tint.

This nucleus lies just below the ependyma of the ventricle, except where (farther brainwards) it is pushed more deeply into the medulla by the chief nucleus of the auditory nerve. Its small cells, which are for the most part spindle-shaped, form a compact rounded group. Roundish darkly-pigmented cells are found on the periphery of this nucleus, especially in the more dorsal parts. Possibly, however, these belong rather to the vagus nerve.

(2) In sections just below the pons, on the dorsal side of the root-fibres



just described and the ventral side of the corpus restiforme, we meet with a thick homogeneous bundle of fibres, *IXa* (figs. 136, 137), the **spinal glossopharyngeal root** (ascending glossopharyngeal root, Stilling's fasciculus solitarius, "respirations-bundel" of Krause, ascending vagus root, trineural fasciculus of Spitzka, descending vago-glossopharyngeal root, etc.). At first it runs parallel with the former, but before reaching the dorsal vagus nucleus it turns suddenly spinewards, and we meet with it in all succeeding sections down to the lower end of the decussation of the fillets. In cross-section it appears as a conspicuous round area, growing smaller by degrees until it finally vanishes. Throughout its vertical course it is accompanied by small masses of grey substance, which lie partly on the periphery of the bundle and partly among its fibres. Histologically this grey substance (the glossopharyngeal nucleus of Roller, vertical glossopharyngeal nucleus) closely resembles the substantia gelatinosa which we have already noticed surrounding the spinal trigeminal root. It reaches its greatest extension at the bend of the root and accompanies it on its horizontal course, but rapidly diminishes in quantity a little farther brainwards.

The spinal glossopharyngeal root invariably lies laterally to the dorsal vago-glossopharyngeal nucleus and dorso-laterally to the roots of the vagus and glossopharyngeal, which enter here. It is sharply circumscribed by the medullated fibres which encircle it everywhere except on its ventral margin.

We may take it for granted that the fibres of this root bend over gradually into the adhering masses of grey substance, the vertical glossopharyngeal nucleus, and end among its cells. They may perhaps previously give off collaterals to it.

*Ramón y Cajal* thinks that all the fibres which diverge to this nucleus are collaterals, and that all the stem-fibres extend to the spinal end of the bundle and terminate in a group of cells lying in the middle line behind the central canal (the ganglion commissurale). The fact that the fasciculus solitarius steadily becomes poorer in fibres as it approaches the cord clashes with this theory, and proves that only a part of the bundle can end in this way. It is probable, on the other hand, that most of the spinal fibres find their destination in the posterior horn, and, perhaps, in the nucleus cuneatus (*Cramer*).

Other root-bundles enter the vertical glossopharyngeal nucleus where it projects above the bend of the fasciculus solitarius. These must not be looked upon as a part of the glossopharyngeal nerve; they may belong to another nerve-root, the nervus intermedius Wrisbergi (*cf.* p. 365), which pierces the substance of the medulla oblongata between the facial and auditory nerves. The extent of the region it occupies has yet to be determined.

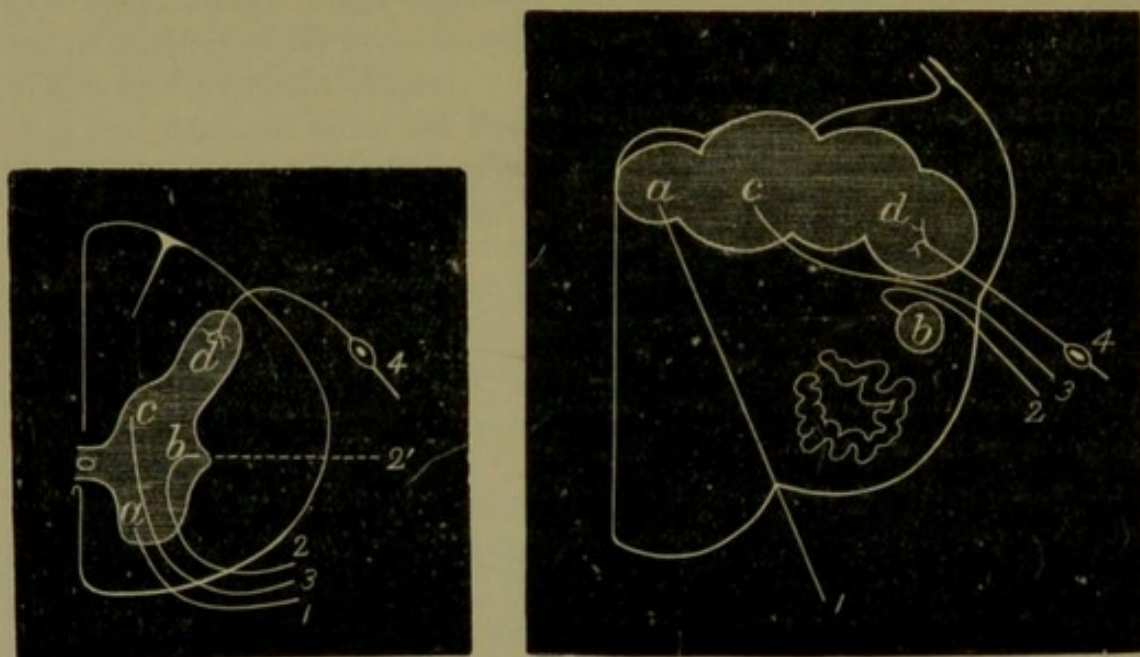
It is very doubtful whether any fibres from the vagus unite with the fasciculus solitarius. We are positively certain that the bulk of the fasciculus takes rise from the glossopharyngeal nerve; the accession from that quarter, therefore (if it exists at all), must be limited to a few isolated fibres.



(3) Large-celled glossopharyngeal nucleus, *Na* (motor or anterior glossopharyngeal nucleus, anterior column of origin of the mixed lateral system, nucleus ambiguus, nucleus lateralis medius). Large cells lie scattered about in the substantia reticularis grisea on the ventral side of the small-celled nucleus of the glossopharyngeal nerve. They are similar to the anterior horn cells of the spinal cord. From these cells fibres, not united into bundles, extend dorsally. Some of these fibres bend round in a latero-ventral direction in sharp curves, and join the glossopharyngeal nerve on its mesial side (*cf.* also fig. 171, *X*). Another set, fewer in number, bend towards the middle line, just before they reach the floor of the fourth ventricle, cross the raphe, and join the glossopharyngeal root of the opposite side. This large-celled nucleus of the glossopharyngeal nerve, which is to be looked upon, as already explained, as a remnant of the anterior horn cut off by the crossing of the pyramids, finds its serial continuation upwards in the facial nucleus, in which the grey masses are more compact, and ends above in the motor nucleus of the fifth. Fig. 171 shows this succession of motor nuclei. [The *translator* has put forward the theory that in the medulla oblongata the anterior horn is truly withdrawn to the mid dorsal line, where it gives origin to the hypoglossal and sixth nerves, and that these nuclei (whether the nucleus ambiguus belongs to the same group as the antero-lateral nucleus of Clarke requires further elucidation), including the nucleus of origin of the spinal accessory nerve, are to be looked upon as the continuation upwards, not of the anterior, but of the lateral horn. It was with a view to obtaining light upon the problem of the segmentation of the head and the morphological value of the cranial nerves, as indicating the limits of its metamers—the vertebræ composing the skull was the aspect of the problem as introduced by *Oken*—that the *translator* hoped to find indications of segmentation in the position of the nuclei within the cerebro-spinal axis. It had for a long time been allowed that nerves are the most conservative organs of the body and longest perpetuate structural dispositions which other organs have discarded, but no attempt had, at the time, been made to look for evidences of metamerism in the nuclei from which the cranial nerves grow. The division of the grey matter in the spinal cord into anterior and lateral columns (horns) of large cells, as well as Clarke's column and the posterior horn, is obvious; and the question which must be settled before attempting to homologise cranial and spinal segments is this—What is the meaning of the distinction between anterior and lateral horns? The answer to this question is given in the cervical region, where the two horns give origin to distinct nerves—the spinal accessory appropriating the lateral horn to itself. This is the key to the problem of the segmental disposition of the cranial nerves—for the seventh and motor part of the fifth, both in line of exit and in position of nuclei, are the successors of the spinal accessory in the occupation of the lateral vesicular column. The division of the cranial nerves into two lines was noticed by *Sir Charles Bell*, who supposed that the lateral group (in which he included the phrenic, the external respiratory of Bell, and the fourth) are thus disposed, on account of their participating in



common in the function of respiration. Another change in the arrangement of the nerves also marks the medulla. The vagus nerve takes origin in the brain (few of the cranial nerves can be justly termed *pure* nerves) from a group of cells which is, as *Ross* pointed out, a local enlargement of Clarke's column at its upper extremity. Here, then, in the medulla we find that each segmental nerve is split up into four elements, anterior motor, lateral motor, visceral, and sensory, which, in the nerves of the spinal cord, are united into a single trunk (figs. 173 and 174). On this basis the *translator* grouped the cranial nerves for the purpose of making up the complement of each single metamer, bearing in mind, however, that, as already remarked, the cranial nerves are seldom pure nerves; even when



Figs. 173 and 174.—Diagrammatic section of the spinal cord and medulla, designed to show the relative positions of the centres in the central grey tube of the several roots of a spinal and segmental cranial nerve respectively; as also the grouping of the constituents of the roots.—*a*, Anterior horn; *b*, lateral horn; *c*, Clarke's column; *d*, posterior horn; 1, anterior (somatic) motor root or nerve; 2, lateral splanchnic (motor) root, which in the lower spinal cord joins the anterior root, in the upper spinal cord runs by itself as 2', the spinal accessory, while in the medulla it accompanies the posterior root; 3, visceral root; 4, the posterior or sensory root bearing a ganglion. The spinal roots unite into a common trunk. With the exception of those of the trigeminus, the cranial roots do not form permanent associations.

fibres of one function greatly preponderate, any nerve may contain the vestiges of nerves of other function. To what extent associations and dissociations have thus occurred the comparative anatomist must decide. Thus much, however, may be accepted as a basis for morphological speculation: the cranial nerves, when called in in evidence of cranial segmentation, must no longer be arranged in linear series of equal segmental value, as was done by *Balfour*, *Marshall*, *van Wijhe*, and others; but must be collected into groups, as in *Gegenbaur's* scheme, although on different lines.

*Gaskell* has taken up the *translator's* scheme, and seems to have carried



it to a very fruitful issue, by showing that fibres from the visceral and the lateral columns of cells tend to travel in company to the splanchnic portions of the body, while the fibres from the cells of the anterior column go to the somatic muscles. As must already be abundantly apparent, even the most fundamental problems in the anatomy of the nervous system are not to be settled with scalpel and forceps, or with the microscope and series of sections; but physiological experiment and morphological speculation are alike called into requisition for the purpose of cutting paths from which to commence purely topographical explorations into the labyrinth.]

A certain harmony in the course of these root-fibres attracts attention. Facial, as well as glossopharyngeal roots (including the vagus) do not take the most direct road to their points of exit, but turn dorsally first. We may conclude from this disposition of the facial fibres that we are right in supposing that the motor glossopharyngeal fibres originate in the large-celled nucleus. The important connection of the nucleus with the root of the opposite side, suggests the view that the muscles which the nerve innervates (stylopharyngeus and constrictor muscles of the pharynx, for example) act bilaterally and simultaneously. There is a slight uncertainty about the innervation of some of the muscles attributed to this nerve.

*Holm* divides the nucleus ambiguus into a lateral and a dorso-mesial part, the latter being the larger.

*Ramón y Cajal* describes fibres which bend off dorsalwards from the motor root and can be followed into the spinal trigeminal root. The physiological meaning of these is uncertain.

According to *Edinger*, the vagus and glossopharyngeal nerves receive an accession (not numerically very considerable) of fibres by way of the direct sensory cerebellar tract (p. 201). The same observer has been able to demonstrate that the fibres which curve out from the ventral side of the sensory nucleus pass into the contra-lateral fillet. This would constitute the connection between the sensory portion and the great brain. The motor cerebral glossopharyngeal tract is probably established by arcuate fibres which cross in the raphe and join the pyramids.

There can be no question as to the motor functions of the fibres from the nucleus ambiguus. *Marinesco* is of opinion that the nucleus ambiguus supplies transversely striped muscles, and that centrifugally-conducting motor fibres for smooth muscles originate from the dorsal nucleus. With regard to the other roots, the striking similarity of the spinal trigeminal root and the fasciculus solitarius must be pointed out. One may suppose that the latter serves to convey the sensory impressions of common sensation which come from the glossopharyngeal area.

Degeneration of the spinal glossopharyngeal root, on one side or both, is comparatively common in tabes and syringo-myelia. It is usually coupled with degeneration of the spinal trigeminal root.

An abnormality of frequent occurrence, known as Pick's bundle, must not be confounded with the spinal glossopharyngeal root. In cross-section this bundle appears as an almost circular column, never much larger than the spinal glossopharyngeal root, but often of the same size or smaller. It



comes into view where the decussation of the pyramids is at its height, and lies mesially and ventrally to the substantia gelatinosa of one side only. Later it is always found on the ventral side of the spinal glossopharyngeal root, and finally reaches the dorsal side of the facial nucleus. Its upper end cannot be determined; in many cases it disappears from the cross-section at a low level.

Disease of the nuclei of the glossopharyngeal nerve is usually hard to recognise. This is especially the case with the nucleus ambiguus, which forms no sharply defined group. It has been observed to degenerate in bulbar paralysis and in amyotrophic lateral sclerosis (*Oppenheim*).

**10. Vagus Nerve (pneumo-gastric nerve, wandering nerve, nerve of the lungs and stomach).**—There is very little to add to what has already been told about this nerve in connection with the glossopharyngeal.

The vagus nerve gets its fibres from the same source as the last-described nerve and ends in the same fashion. Only the spinal root is lacking, or represented by a few isolated fibres which join the fasciculus solitarius.

The sensory root of the vagus ends in the dorsal vagus nucleus, which lies in the floor of the fourth ventricle and (in sections farther spinewards) beneath the central canal. The motor fibres originate from the nucleus ambiguus of the same side and receive a contingent from that of the opposite side.

*Holm* distinguishes three groups of cells in this nucleus, a ventro-mesial group of large cells (respiratory cells), a dorso-lateral group of smaller cells (centre for tracheal reflex), and, finally, those in the part nearest to the fasciculus solitarius. He assigns the last group to the glossopharyngeal nerve, under the name of sensory glossopharyngeal nucleus. We must, however, suppose that the sensory glossopharyngeal fibres which do not enter the fasciculus solitarius find their destination in the proximal parts of the sensory vago-glossopharyngeal nucleus.

In most fishes the vagus nucleus attains a very remarkable development; the reason being that the lateral organs—the peculiar sensory organs which can be followed to the tail-end on either side—are supplied by a branch of the vagus nerve, the nervus lateralis.

*Holm* asserts that he has frequently observed slight sclerosis in the region of the sensory vagus nucleus, and by means of such observations has arrived at the above conclusions. Grave and conspicuous pathological changes in the central regions of this nerve (affecting both nucleus and roots in tabes) are very seldom met with. This was to be expected, since the extremely important part played by this nerve in functions essential to the maintenance of life, such as circulation and respiration, adds an element of serious danger to diseases otherwise comparatively trifling.

**11. Accessory Nerve (accessorius Willisii, nervus recurrens, nerve of the leg, spinal nerve).**—It is customary to describe two different modes of origin for the accessory nerve, which is a motor nerve pure and simple. The proximal or superior part of the root-bundle comes out as a continuation of the vagus origin, between the olive and the corpus restiforme, accessorius vagi (*seu* cerebralis), XI (fig. 10). The distal or inferior portion of the nerve, accessorius spinalis, arises by a row of root-



filaments from the lateral surface of the medulla oblongata and cord on the outer side of the posterior roots, from the level of the lowest roots of the hypoglossus down to the fifth or sixth (and, exceptionally, the seventh). The accessorius vagi has exactly the same origin as the vagus itself, from which (on the surface of the brain) it cannot be separated. *Kölliker* assigns to the accessory nerve the more distal bundles, which issue on the ventral side of the spinal trigeminal root, and to the vagus the upper bundles which break through it; since the union of the last-mentioned fibres with the accessory trunk is merely temporary and in their extra-cranial course they join themselves definitely with the vagus; so that it is best to speak of them as the most distal vagal roots, and to restrict the term accessory to the spinal roots which are purely motor.

In many sections taken from the upper part of the cervical cord a strong curved bundle, convex dorsally, is seen to enter the lateral column (at a spot the relation of which to the point of exit of the posterior roots varies), to



Fig. 175.—Diagram showing the disposition of the nervus accessorius Willisii in cross-section.—*n*, Cells of origin; *v*, respiratory bundle; *XI r*, issuing root; *rp*, posterior, *ra*, anterior spinal roots.

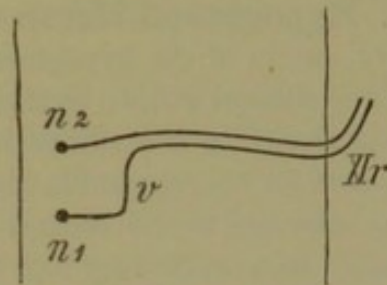


Fig. 176.—Scheme showing the disposition of the n. accessorius Willisii in longitudinal section.—*n1*, *n2*, Cells of origin; *v*, ascending segment of the root (Krause's respiratory bundle); *XI r*, issuing root.

traverse the lateral column and pass into the grey matter in the region of its processus reticularis (figs. 132 and 173). At the level of the decussation of the pyramids it is often difficult to distinguish the roots of the accessory nerve from those fibres of the lateral column which are making their way obliquely towards the middle line.

These fibres take rise from motor cells situate in the dorso-lateral region of the anterior horn and either course in the same transverse plane straight to the lateral column (fig. 176, *n2*) or reach it after first running longitudinally for a certain distance within the grey substance, *v* (figs. 175 and 176). The nerve-cells just mentioned are, therefore, considered to constitute the proper accessorius nucleus, *n1* and *n2*.

The account just given (after *Roller*) corresponds best with the facts, but other very divergent views as to the origin of the accessorius are held.

The cells of the lateral horn, as well as those of the processus reticularis, have been claimed as the accessorius nucleus. That fibres which come from the other side of the medulla join the root-bundles is most probable. *Roller* allows the accessorius a further accession in fibres which arise in the



lateral column, while *Darkschewitsch* describes fibres which reach the accessorius from the nucleus of Burdach's column.

Just as little uniformity reigns amongst the accounts given with regard to the level in the cord from which the accessory fibres arise. Many think they arise from the lateral horn throughout the whole length of the cord (*Krause, Clarke*), which is certainly not the case; others only as far as the fifth cervical (*Huguenin*).

*Dees* agrees in the main with *Roller*, but makes more exact statements as to the position of the nucleus accessorius. This group of cells lies, he says, in the middle of the anterior horn on the cerebral side of the first cervical nerve; at the fourth cervical nerve it has moved back to the lateral border of the anterior horn; and from there to the sixth cervical it remains at the base of the lateral horn. The vertical segment, *v*, which many of the root-bundles present, lies, according to *Dees*, in the angle between the anterior and posterior horns; perhaps, therefore, it corresponds with *Krause's* respiratory bundle. *Staderini* and *Pieracini* think that they can prove the existence of a sensory portion of the spinal accessory nerve.

**12. Hypoglossal Nerve.**—The most important (and in all probability the only) origin of the hypoglossal nerve is from a grey area on the ventral side of the central canal; farther brainwards it lies in the floor of the fourth ventricle alongside the sulcus longitudinalis; the spinal portion is, at the decussation of the pyramids, the only portion of the anterior horn which remains attached to the central grey matter. It is characterised by large multipolar nerve-cells very like ordinary anterior horn-cells. The dendrites of these cells have been followed sometimes, it is said, to the contra-lateral nucleus (protoplasmic hypoglossal commissure of *Ramón y Cajal*). This grey column, which can be followed as it lies up against the raphe as far brainwards as the striæ medullares, is termed the large celled nucleus of the hypoglossal nerve, *NXII* (chief nucleus, *Stilling's* classical hypoglossal nucleus, figs. 134 to 145, 154 and 171). Globular spots, sometimes as much as 1 m. in diameter, enclosed in a closer network of medullated fibres, are occasionally met with in the hypoglossal nucleus. They contain a great many very small nerve-cells and but few medullated fibres; and are therefore conspicuous in *Weigert's* preparations as light spots in a dark frame. The coarse hypoglossal fibres show many twistings and curvings inside this nucleus, on a close ground-network of fine fibres. United into thick bundles they extend thence to its point of exit on the outer side of the pyramids. In exceptional cases a bundle may pass straight ventralwards, forcing its way through the pyramids, and issuing from them on to the surface, where it usually lies in an abnormal shallow sulcus. The most distal fibres are directed brainwards in a remarkable degree, so that they do not in our sections show their whole length (fig. 134). The lower olives are traversed by many hypoglossal fibres which come into no anatomical connection with them; the fibres suffer thereby, however, a number of distortions from their otherwise rather straight course, both in sagittal and in frontal planes. In most animals the exit of the hypoglossal nerve lies on the lateral side of the olives.



The mesial angle of the large-celled hypoglossal nucleus is occupied (in the upper or cerebral half) by a rounded column of small cells of unknown meaning; we have already met with it in the chief auditory nucleus as the nucleus medialis or nucleus funiculi teretis. On the lateral side of the hypoglossal nucleus we meet with another group of small cells (nucleo intercalato of Staderini), which separates it from the dorsal vago-glossopharyngeal nucleus. It is also confined to the cerebral half.

A second origin is from the small-celled hypoglossal nucleus of Roller. By this is meant a not distinctly circumscribed round clump of small nerve-cells which lies close up against the ventral side of the large-celled nucleus; in the sections farther brainwards it surrounds the root-bundles of the hypoglossus. It is, however, very unlikely that hypoglossal fibres originate from this somewhat inconstant group.

It has also been asserted that the large multipolar cells which are seen in the substantia reticularis in the neighbourhood of the hypoglossal roots (belonging to the nucleus lateralis medius), also give an accession of fibres to them (*Duval, Koch*). *Laura* regards the nucleus ambiguus as an accessory nucleus of this nerve. Neither suggestion appears to be borne out by the facts.

Some of the root-fibres when just to the ventral side of the nucleus bend towards the middle line joining the beautifully arched bundle which originates in part from the hypoglossal nucleus and in part from the dorsal vago-glossopharyngeal nucleus, and crosses the root-bundles which issue from the ventral side of the former. If any root-fibres cross from the nucleus of the opposite side, it is here that we should look for them.

Commissural fibres between the two nuclei seem to be present, as well as fibres which take part in the formation of the posterior longitudinal bundle.

The central tracts of the hypoglossal nerve pass from its cortical centre in the pars opercularis of the temporal lobe, over the upper border of the nucleus lenticularis, to the genu of the capsule. Interruption of this bundle is said to interfere with the motility of both sides of the tongue (*Edinger*). Farther down, the hypoglossal tract probably lies between the facial tract and that which supplies the extremities. We may also suppose that in the lower region of the pons the hypoglossal fibres occupy the most mesial parts of the pyramidal tract, and then abandon their longitudinal course and bend dorsalwards, cross in the raphe, and sink as fibres of the corona radiata into the ventral side of the hypoglossal nucleus to surround the large nerve-cells contained in it. In the rabbit the central hypoglossal tract crosses at the level of the nuclei of origin of these nerves.

Numerous fine fibres (*fibræ radiales internæ*) converge to the hypoglossal nucleus (*Kölliker*). Starting from somewhere near the olives, they traverse the substantia reticularis grisea, and break up in the hypoglossal nucleus. *Kölliker* was unable to determine whether they took rise in the olive or the pyramid. Other fibres which stream radially into this nucleus must be classed as sensory conducting fibres or collaterals from the region of the vagus, glossopharyngeal, and trigeminal nerves.



Various connections with other parts of the brain appear to be established by means of the fibres of the medullary layer which, lying dorsal to the hypoglossal nuclei, gives the white colour to the floor of the ventricle, *m* (figs. 137 and 154). Many of these fibres bend laterally and unite into a strong column which traverses the vagus nucleus and ends in an unknown manner. *Koch*, who looks upon this stratum as made up chiefly of fibres connecting the different cells of the hypoglossal nucleus to one another, speaks, consequently, of *fibræ propriae nuclei hypoglossi*; he thinks, however, that commissural fibres also go out from them. But these fibres probably belong to a system of longitudinal fibres which can be followed in the floor of the fourth ventricle and up to the third, the dorsal longitudinal bundle of *Schütz* (not to be confounded with the posterior longitudinal bundle). It is especially thick and conspicuous in the vicinity of the hypoglossal nucleus. It may perhaps serve to establish a connection between the different levels of the central cavity. Small nerve-cells, belonging to the *nucleo intercalato* of *Staderini*, already mentioned, are found in the lateral part of this bundle. This group of cells is supposed to pass over into the triangular auditory nucleus higher up.

Disease of the hypoglossal nucleus is usually easy to recognise, since the intra-nuclear network of fibres disappears as the nerve-cells decay; though a vestige of it usually remains after they have all come to grief.

The hypoglossal nucleus is also affected in most cases of amyotrophic lateral sclerosis.

A process analogous with the poliomyelitis of the spinal cord may cause destruction of the motor nuclei of the medulla oblongata and the rest of the brain-stem as far as the third ventricle. Ophthalmoplegia nuclearis has been already mentioned. A disease to which the cells of origin of the hypoglossal nerve first fall victims, then those of the facial nerve, as well as the vagus and glossopharyngeal (chiefly their motor nuclei), and exceptionally, also, the cells of the motor root of the trigeminal nerve, is known as glosso-labio-pharyngeal paralysis (progressive bulbar paralysis, poli-encephalitis inferior). The above-mentioned nuclei are occasionally found more or less diseased in tabes.

Both hypoglossal nuclei are affected in almost every case, on account of their nearness to each other. Unilateral nuclear degeneration is met with, as an exception, in cases of embolic softening (*Hirt*) and tabes.

In progressive paralysis the fibres of *Schütz's* dorsal longitudinal bundle are apt to dwindle to a very remarkable extent.

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### C. THE CEREBELLUM.

**I. Central Nuclei.**—We have already discovered that the cerebellum presents a peripheral grey layer or cortex, as well as certain internal masses of grey matter, and various columns of fibres which take part in the formation of its medullary substance.

Reserving the description of the finer histological details for treatment later on, we must now examine the central grey masses of the cerebellum. Neither the corpus dentatum with its appendages (the nuclei emboliformis and globosus) nor the nucleus of the roof, actually reach the surface of the ventricle; but they come very close to it, being separated therefrom by a thin white layer only.

(1) The **corpus dentatum** is a purse-shaped, many-plaited sheet of grey matter surrounding a mass of white substance, distinguished by the numerous large veins which it contains (nucleus medullaris corporis dentati). The opening into the bag is directed forwards and medianwards. The thickness of the grey band is from 0.3 to 0.5 mm.

It contains nerve-cells of one kind only, not very closely packed together, from 20 to 30  $\mu$  in long diameter, and a varying amount of pigment. Most of the cells are so arranged that a single process is directed into the medullary centre, in which it can be followed for a considerable distance; while two or three processes, which divide dichotomously, are directed towards the outer medullary substance of the cerebellum. Numerous medullated fibres not united into distinct bundles traverse the grey matter of the nucleus from without inwards, whilst other fibres, usually of considerable calibre, run through the grey matter itself in a direction parallel with the surface of the sheet. A fairly close network of finer fibres also occupies the whole thickness of the grey matter.



The silver-method of impregnation shows that the cells here have wide-branching protoplasmic processes, and single axis-cylinder processes, difficult to follow. *Ramón y Cajal* thinks that these last pass into the brachium conjunctivum. Thick nerve-fibres are also met with, which enter from the periphery and break up into rich plexuses. These probably take rise in the Purkinje's cells of the cortex cerebelli (*Ramón y Cajal*).

The cells of the corpus dentatum develop very early in the human foetus, being distinctly recognisable between the sixth and seventh months of intra-uterine life.

(2 and 3) **Nuclei emboliformis et globosus** are only separated pieces of the corpus dentatum, which they resemble in structure.

(4) The **nucleus of the roof**, *Nt* (nucleus tecti, nucleus fastigii, substantia ferruginea superior, figs. 15, 16, 177), is to be looked upon as the central nucleus of the vermis. It has a not well-defined triangular or oval form, and is about 6 mm. in its sagittal diameter. Only a thin layer of medullary substance separates it from the ventricle. It reaches upwards for about a half or two-thirds of the thickness of the vermis. It is least well-defined at the back. In the median plane it almost reaches the nucleus of the roof of the opposite side. Large vesicular ganglion-cells (40 to 90  $\mu$  in diam.), containing a great deal of yellow-brown pigment, are found in it, as well as numerous nerve-fibres, many of which (united into coarse bundles) extend transversely across to the nucleus of the opposite side, *Dt* (decussation of the nucleus of the roof). We know nothing for certain about the course and ultimate fate of these fibres. Remarkably thick axis-cylinders (5  $\mu$  in diam.) are met with also, as well as quantities of granules.

Lastly, we must notice certain small grey clumps which, if great care is used, can be found in many cerebella in the midst of the medullary substance. Usually they are very small, scarcely visible, or at any rate not larger than a grain of millet; but, exceptionally, they may attain to a diameter of 1 cm. They contain, besides a network of fibres, regularly-disposed, club-shaped nerve-cells, very similar to Purkinje's cells; also granules like those of the granular layer and a close capillary network (fig. 187); and must therefore be looked upon as separated pieces of cortex. *Pfleger* first called attention to the frequent occurrence of these small heterotopic collections of cortical substance.

The same central grey masses are found in animals, but the corpus dentatum is never so much plicated as in Man; even in monkeys it is relatively a broader and less folded sheet, while in lower mammals it is merely a diffuse grey mass. In birds, in correspondence with the considerable reduction in the size of the cerebellar hemisphere, only a single roof-nucleus is present; it is covered with a thin sheet of medullary substance, and bulges out on either side into the dorsal prolongation of the fourth ventricle, which is a characteristic feature of the cerebellum in birds. There are, however, lateral groups of nerve-cells, which may be regarded as representing the corpus dentatum. Even in fishes two nuclei are discernible in the medullary substance on either side, although



the cerebellum shows not the slightest indication of division into hemispheres (*Ramón y Cajal*).

**2. The Medullary Substance of the Cerebellum.**—Three mighty columns of fibres, as well as certain other tracts of less dimensions, converge from either side to form the medullary mass of the cerebellum.

The origin of the **corpus restiforme** has already been explained (p. 312); we have also described the way in which the spinal constituents of the corpus restiforme turn into the vermis of the cerebellum, the fibres of the two sides crossing one another apparently in the 'anterior commissure and decussation,' and how the portion of the restiform body derived from the olive loses itself in a plexus of fibres which envelops the corpus dentatum in a kind of coat, the 'fleece' of *Stilling*.

It may be inferred from the results of *Monakow's* investigations, that the portion of the corpus restiforme which ends, without crossing, in the cortex of the vermis, comes from the lateral cerebellar tract. *Vejas* denies that any part of the restiform body crosses in the cerebellum. *Auerbach* thinks, nevertheless, that the bulk of the ventral portion of the cerebellar tract goes to the opposite side of the vermis superior, and that only fibres from its dorsal portion end, for the most part, on the same side.

Many fibres of the restiform body probably reach the cortex cerebelli.

Owing to the directly anterior course of the corpus restiforme the fibres intended for the back of the cerebellum must bend off at an acute angle ('neck of the cerebellar peduncle').

The fibres which enter the cerebellum by the **pedunculus pontis** (or pass into the pons from the cerebellum) are disposed in thin plates which split off from the main mass as the several branches and twigs of the 'arbor vitæ cerebelli.' It seems as if the whole of the cortex, both of the hemispheres and of the vermis, is plentifully supplied with pontine fibres. A crossing of these fibres in the vermis is not proved. Possibly the capsule of the corpus dentatum receives fibres from the pons. A more detailed account of the disposition of the fibres of the pons has been already given (p. 303), and it has been already pointed out that they probably provide for a crossed connection between the cerebrum and cerebellum.

The third connection of the cerebellum extends brainwards, the **brachium conjunctivum** (superior cerebellar peduncle, crus cerebelli ascendens, processus cerebelli ad corpora quadrigemina seu ad cerebrum, brachium copulativum).

Almost all the fibres from the centrum medullare corporis dentati pass out of the hilum into the brachium conjunctivum, of which they constitute the most important components. They are termed its intra-ciliary constituents, as coming from the 'corpus ciliare.' The brachium conjunctivum also contains extra-ciliary fibres, derived from the fleece, as well as a few, perhaps, from the cortex cerebelli, especially the vermis. When its fibres are first collected into a bundle the brachium lies on the mesial side of the corpus restiforme (*cf.* fig. 142). Just below the ependyma at the lateral angle of the ventricle lies a bundle which can be easily unravelled; it joins the brachium conjunctivum and runs brainwards with it as far as the



locus cœruleus, with which it is always connected. Its presence is to be associated with the fact that we can always find within the brachium conjunctivum (especially when we make our sections in the long axis of this column) a number of spindle-shaped cells of as much as 90  $\mu$ m. in diameter and containing dark-brown pigment. These fusiform cells are laid with their long axes in the direction of the fibres. The bundle is known as the lateral longitudinal bundle of the roof of the ventricle. At their spinal end these fibres seem to turn, just in front of the striæ acusticæ, on the dorsal side of the corpus restiforme, outwards towards the stalk of the flocculus. Concerning the connections of the brachium conjunctivum with the auditory nerve, see p. 372.

As the brachia conjunctiva coming out of the substance of the cerebellum converge toward the corpora quadrigemina they are covered by the inferior (lateral) fillets which come up from the outer side. They further show a tendency, as we have seen (figs. 134 to 138), to draw ventralwards and towards the middle line, and between the posterior and anterior quadrigeminal bodies they begin to cross. The decussation is at its height beneath the centre of the anterior quadrigeminal bodies (decussation of the brachia conjunctiva, Wernekinck's commissure, tegmental decussation). The greater part of the brachia certainly cross here, but it has been already stated that they contain fibres which do not take part in the decussation (*Mendel, Bechterew*). It has also been supposed that in the posterior angle of the decussation are situate fibres which are commissural between the two cerebellar hemispheres, connecting together (that is to say) the two nuclei of origin of the auditory nerves.

After their crossing, the brachia conjunctiva extend, as round columns ([once called] the white nuclei of the tegment), a short distance farther brainwards; soon, however, they swell out owing to the intercalation of small pigmented nerve-cells into a mass, also round in cross-section (figs. 148, 149, 150, 154), which in the fresh state is light brown in colour, the red nucleus of the tegment (nucleus ruber tegmenti, olive supérieure of *Luys*). We still need a more detailed account of the histology of the red nucleus. The fibres which pass out of it are collected into small bundles while still within its substance, giving to it a peculiar striped or punctate appearance. We may take for granted that some of the fibres of the brachium conjunctivum pass through the red nucleus without interruption.

It is not possible to give a really satisfactory account of the fate of the fibres which leave the red nucleus. Most probably these fibres lose themselves in the ventral part of the optic thalamus, as described by *Forel*. Some of them go, perhaps, to the cortex cerebri, most probably to the central convolutions (*Flechsig* and *Hösel*), and some, possibly, to the nucleus lenticularis.

The fact that the brachium conjunctivum degenerates completely after the destruction of one hemisphere of the cerebellum (*Ferrier* and *Turner*) justifies us in giving preference to the view that the majority, at least, of the fibres which compose it originate in the cerebellum and conduct brain-



wards, in spite of some observations which might lead to the opposite conclusion (*cf.* p. 398).

Other connections of the cerebellum, besides the three peduncles, also exist. Cerebellar roots of several cranial nerves have been described (direct sensory cerebellar tract of *Edinger*), but in no case are they certainly proved. Possibly the sensory root of the fifth receives an accession from the medullary centre of the cerebellum (*cf.* p. 358). The fibres which have been indicated as the cerebellar root of the auditory nerve are, probably, only secondary connections between the cerebellum and the large-celled nucleus of the nerve (fig. 149). Some of the fibres, probably, reach the roof nucleus of the opposite side. On either side of the middle line a thin tract of fibres, *frenulum veli medullaris anterioris*, passes out of the

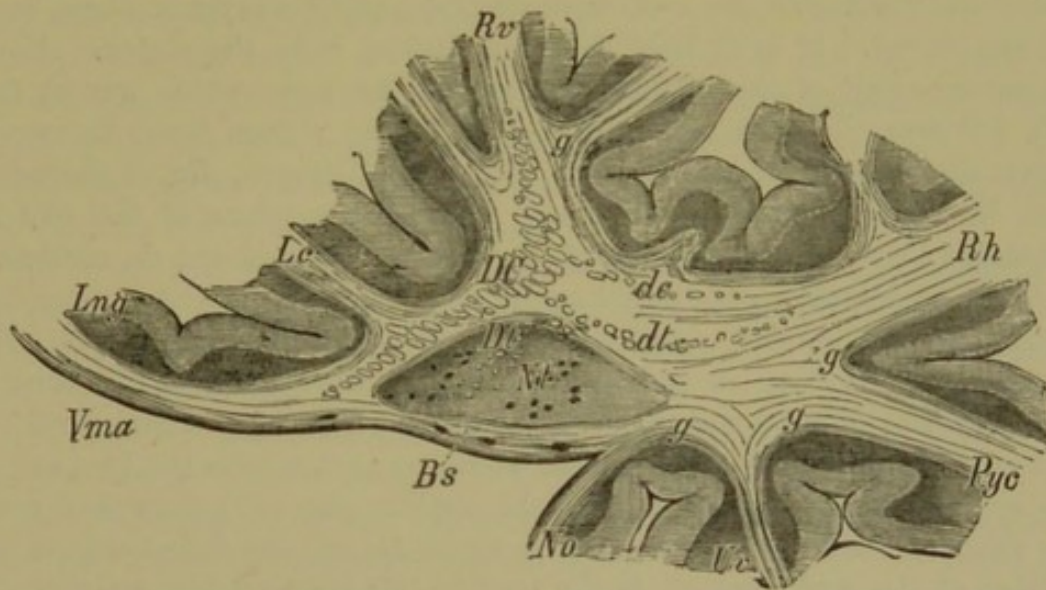


Fig. 177.—Sagittal section through the cerebellum some millimeters to one side of the middle line. *Magn.* 5.—*Vma*, Velum medullare anterius; *Lng*, lingula; *Lc*, central lobule; *Rv*, vertical medullary ramus; *Rh*, horizontal ditto; *Pyc*, pyramis cerebelli; *Uv*, uvula; *No*, nodulus; *Bs*, sagittal basal tract; *DC*, anterior great commissural decussation; *dc*, its posterior prolongation; *Nt*, nucleus of the roof; *Dt*, decussation of the nucleus of the roof; *dt*, its posterior prolongation; *g*, garland-like fasciculi.

region of the corpora quadrigemina into the cerebellum in the velum medullare anterius, beneath the lingula.

Several divisions of the **medullary centre** of the cerebellar hemispheres may be described: (1) the medullary centre of the corpus dentatum; (2) the 'fleece' or plexus of fibres which stands in intimate relation with the corpus dentatum, enclosing it, in fact; (3) *Stilling* has described certain different sets of fibres in the remaining greater mass of the white matter which are very difficult to distinguish; (4) a layer, 0.2 to 0.5 mm. in thickness, which lies in contact with the inner layer of the cortex of the cerebellum, following its contour, the 'garlandlike' bundle which connects the different lobules together, *g* (fig. 177); (5) in sagittal sections numerous bundles of fibres are seen cut across in front (brainwards) of the corpus dentatum, they belong to the great cerebellar commissure; other



bundles are cut across on the dorsal side of the corpus dentatum above the 'fleece'; they constitute the dorsal cerebellar commissure.

The **medullary centre of the vermis** (fig. 177) is often called the corpus trapezoides, a name which should be avoided, since it belongs to a different structure. A sagittal section through this mass shows the nucleus of the roof, *Nt*. This nucleus lies on a layer of sagittal fibres (median sagittal basal-bundle, *Bs*), which can be followed brainwards into the fibres of the velum medullare anterius, *Vma*. On either side it is joined by the lateral longitudinal bundles of the roof of the ventricle. Single dark pigmented nerve-cells are also found between the fibres of these bundles.

The **large anterior commissure**, *DC*, is met with on the cerebral side of the nucleus of the roof, separated from it by a layer of fibres, some 0.2 mm. broad. It is at least 0.4 mm. distant from the cortex. Above the anterior half of the nucleus of the roof the layer, which was at first only 0.2 mm. in thickness, increases to 1 mm.; from here it extends, always diminishing in size, far into the vertical branch, *Rv*, of the arbor vitæ, in which it ends in a point. Above the nucleus of the roof an indistinctly curved continuation of the anterior commissure, *dc*, consisting of separate bundles, cut transversely, can be followed close under the cortex, as far as the commencement of the horizontal branch, *Rh*. Especially in its most strongly-developed part the anterior commissure is split by fibres which come out of the anterior border of the nucleus of the roof into bundles which are fusiform when cut across, with the long axis of the spindle placed sagittally. Frontal sections (fig. 145) show that not a few fibres of the anterior commissure, which lie on the dorsal side of the nucleus of the roof, descend in the median line between the nuclei of the two sides, cross one another here, and then, apparently, assume a sagittal course.

The **commissure of the roof nuclei**, *Dt*, consists of a second set of fibres, independent of the anterior commissure. We have already mentioned that numerous round bundles run from one side to the other within the substance of the nuclei of the roof; they are most numerous, perhaps, in their anterior portions. These rounded bundles of fibres also form the dorsal boundary of the nuclei of the roof and are arranged in a gently-sloping line, so that the last of the bundles are found in the beginning of the horizontal branch. The latter portion of the roof commissure, *dt*, is nothing more than the middle portion of the dorsal cerebellar commissure.

Behind (distalwards to) the nucleus of the roof no transverse fibres united into bundles are found in the medullary centre; some such are found, however, far back in the horizontal branch where it breaks up into a number of smaller branches (posterior cerebellar commissure). Longitudinal fibres are found almost exclusively in the medullary branches of the arbor vitæ, so that they lie in the plane of sections cut at right angles to the convolutions. Sections must be strictly sagittal when the vermis is cut, while for the hemispheres they should diverge to the sides posteriorly.



These longitudinal fibres lie in the centre of each medullary branch directed towards the general medullary centre; on the other hand, the garland-like tracts of fibres above mentioned lie up against the cortex. In all places where the medullary branches divide dichotomously, or where lateral branches come off from them at right angles, a thickening of the medullary substance, due to an increase in its gleia-tissue, is visible. In stained sections these spots are coloured more deeply on account of this preponderance of gleia-tissue.

The following **connections** of the cerebellum are almost certainly established; others, not sufficiently determined as yet, may also exist:—

(1) With the spinal cord and the after-brain by means of the corpus restiforme.

(a.) With the lateral cerebellar tract, and so with Clarke's column and the posterior roots of the same side.

(b.) With the nuclei of the posterior columns of the same and the opposite side, and, therefore, indirectly with the posterior roots of both sides.

(c.) With the inferior olive of the opposite side.

(2) Only slight connections with the mid-brain through (as is supposed) the frenulum veli medullaris anterioris.

(3) With the 'tween- and fore-brains—(a.) Through the pedunculus pontis, and by means of the contra-lateral pes pedunculi cerebri with the cerebral hemisphere of the opposite side. (A portion of this connection has been described as the frontal pontine tract.)

(b.) Through the brachium conjunctivum with the red nucleus of the opposite side, and thence with the optic thalamus.

(c.) Indirectly with the nucleus lenticularis through the opposite inferior olive and the central tegmental tract.

(4) With certain cerebral nerves; undoubtedly with the auditory, that is to say, with one of the nuclei of origin of the radix vestibularis; probably also with the trigeminus. *Edinger* designates this connection the direct sensory cerebellar tract. According to this authority, we should picture it as a fibre tract which takes rise somewhere near the nucleus globosus and, coursing downwards on the mesial side of the corpus restiforme, gives off most of its fibres to the trigeminal and auditory nerves, and is still further reduced by contributing some fibres to the vagus and glossopharyngeal nerves. The last remnant of it can be followed into the posterior columns of the spinal cord. It would be easier to believe that this tract (which would be almost identical with the spinal auditory root) passes from the sensory nerve-roots to terminate in the cerebellum. According to *Bruce*, the fibres of the pedunculus flocculi can be followed to the nuclei of the nervus vestibularis, nervus cochleæ, and, perhaps, to the nervus abducens.

It appears as if a direct connection between the cerebellum and the anterior roots of the spinal nerves is wanting. One may suppose, however, that the cerebellum is affected by stimuli coming from various sensory regions, and is capable, under the action of these stimuli, of influencing the release of motor impulses.



One momentous question yet to be decided is the localities in which the various cerebellar tracts begin and end. This would determine the direction of their conductivity.

It has been pretty generally assumed that the interciliary fibres, at least, of the brachium conjunctivum pass from cerebellum to cerebrum, originating, therefore, for the most part, from axis-cylinder processes of the cells of the corpus dentatum; but quite recently *Mahaim* and others have maintained that the brachia conjunctiva take origin from the red nucleus and terminate in the corpus dentatum and cerebellar hemispheres. We, however, will abide by the former opinion.

*Kölliker* takes the view that the brachium conjunctivum, crus pontis, and corpus restiforme, must contain fibres of both kinds—those, to wit, that conduct to and those that conduct from the cerebellum—in equal numbers. The difficulty that then presents itself is how to demonstrate the presence in the corpus restiforme of fibres on their way from the cerebellum to the medulla oblongata. We should be forced to assume the existence of nerve-fibres originating from the cells of Purkinje and breaking up into their terminal ramifications in the neighbourhood of the inferior olive (*Held*).

The functions of the cerebellum can be still further explained from the anatomical data given above. Of all sensory impressions it is chiefly those of muscular sensations which are conducted to the cerebellum through the nuclei of the posterior columns (pp. 238 and 312). Further, this organ is intimately connected with the large-celled auditory nucleus from which the greater part of the vestibular nerve arises. We are bound to regard the semicircular canals, after the exact experiments of *Goltz*, *Mach*, *Breuer*, and others, as the organs of the sense of equilibration; the sensations which they set up are transferred directly to the cerebellum for further elaboration.

Impressions of muscle-sense and of equilibration (as well as visceral sensations, which may be conducted to the cerebellum through the lateral cerebellar tracts) do not, so fully as other sensations, help to make up intellectual life; they continually, however, exert an influence on the threshold of consciousness and so modify the movements of the body without needing the intervention of the cortex of the great brain. These sensations find a meeting-place in the cerebellum from which they direct our movements; the necessary force for the production of a co-ordinated movement is probably measured out to each single muscle contraction from this centre. It can hardly be supposed that influences on motility which come out from the cerebellum enter the cortico-muscular pyramidal tracts on their way through the pons, despite the close interweaving of the two systems of fibres, for we are bound to believe that the fibres descending from the cortex to the spinal cord go through the pons without interruption. In all probability, the numerous collaterals which they give off within the pons and which enter the ganglia there, conduct rather from than to the pyramidal fibres. The physiological connection which the cerebellum brings about between certain sensory impressions and motor impulses may, therefore, take place through the cortex cerebri;



or, as is more probable, through other parts of the great brain (fig. 155, C<sup>5</sup>). I may also observe that *Kölliker* thinks the cerebellum more intricate in structure and connections than any other part of the brain.

**3. Cortex Cerebelli.**—If we take a section through one of the lobes of the cerebellum, we shall find that it consists of a central prolongation of the medulla enveloped in grey cortex. Under the microscope we can distinguish three layers in this cortex, the granular layer, which is innermost, then the layer of large cells, and finally the molecular layer, the outermost of all (*cf.* also fig. 182). The boundary between the cortex and medullary substance of the cerebellum is nowhere quite sharply marked; at the summit of the lobules it is quite obscured; it is more distinct at the bottom of the fissures (fig. 178).

The bodies described as 'granules' are found scattered about everywhere between the bundles of white fibres, although sometimes they are arranged in rows. They can be easily distinguished in carmine preparations, or, better still, in those made by some method of nuclear staining. Towards the surface they are more closely packed together, and constitute the **granular layer** ('rust-coloured' layer, since it is marked out macroscopically by its yellow-brown colour). The layer of granules is thinnest at the bottom of the fissure, thickest at the summits of the convolutions.

The granules are not disposed regularly throughout the layer; they always constitute rounded groups where they are most numerous.

If we enquire into the meaning of these granules, we learn (chiefly by the help of the method of impregnating with silver) to class them among cell-elements of different kinds—small nerve-cells (granules) and gleia-cells.

The granules (which have already been mentioned, p. 151) constitute the main part of the granular layer. They are small (from 6 to 10  $\mu$ ) and nearly spherical, with a large nucleus and a very thin envelope of protoplasm (figs. 60, 179, and 182), and possess from three to five dendrites, which quickly break up, in a characteristic manner, into peculiar claw-like terminal ramifications. The axis-cylinder process starts from the cell-body itself or from one of the protoplasmic processes, and goes straight up into the molecular layer. There, as we see in sections taken parallel to the longitudinal axis of the convolution (fig. 179), it divides into two branches, which leave it almost at right angles and so form, as it were, a continuous fibre. These (parallel-fibres) can be followed parallel to the surface for a long distance, though no one has yet succeeded in ascertaining their ultimate fate. They are slightly spiral in disposition and give off no collaterals. The question whether the axis-cylinder processes of all

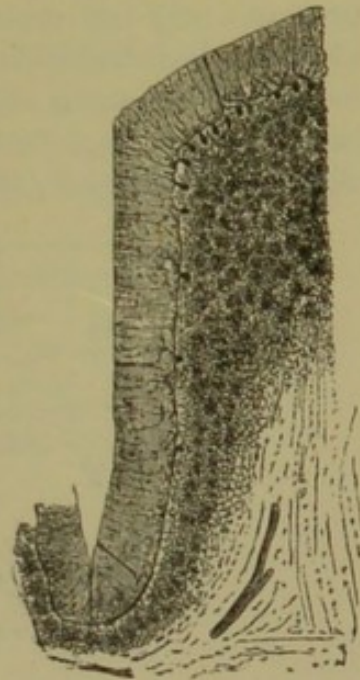


Fig. 178. — Cross-section through a convolution of the cerebellum. *Carmine staining.* *Magn. 15.*



the granules are alike in behaviour must remain open. If we consider the enormous number of granules and the great length of the individual fibres, it is hardly comprehensible that, closely as they are packed in the molecular layer, there should be room for a fibre from every granule.

[The granules are not all of the kind described above, but there are, as the *translator* has discovered, several additional classes of granules which, for want of a better name, he terms 'carrot-granules,' owing to their pyriform shape as compared with the round granules of Golgi. Their size is approximately the same as that of the round granules (*i.e.* 10 to 15  $\mu$ ). They are found in all layers of the cerebellar cortex. Their axis-cylinder processes may run centripetally or towards the periphery, or in the case of those which lie in the molecular layer, tangentially. When the granule lies in the granular layer and its axis-cylinder is centrifugal, it passes between the cells of Purkinje and divides, like that of a round granule, in the molecular layer; if it is centripetal, it branches. The axis-cylinders

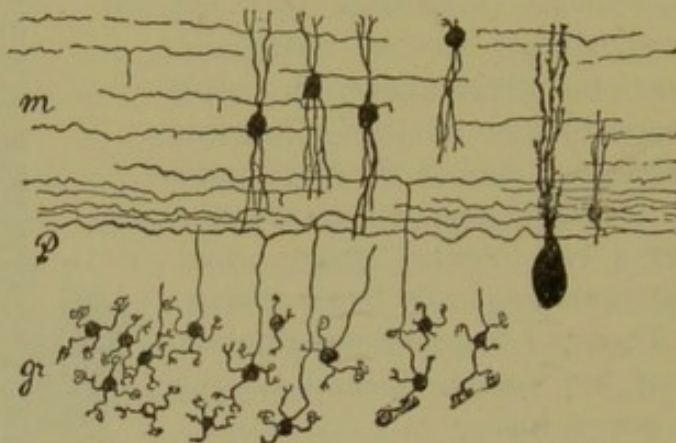


Fig. 179.—Cortex cerebelli of a kitten.—Section parallel to the convolutions. *Silver preparation*.—*gr*, Granular layer; *P*, layer of large cells; *m*, molecular layer.

of the tangentially-placed granules of the molecular layer are marked by frequent branching.]

Most of the remaining nuclei of the granular layer belong to the glia-cells, of which I shall speak later.

Here and there among the granules a few nerve-cells of larger size (from 30 to 40  $\mu$ ) are seen, irregular in shape and usually pigmented. Their number varies in different individuals, but is never large; and the majority of them belong to Golgi's second type (fig. 59). The ramifications of their dendrites may extend far up into the molecular layer or down into the medullary centre. The axis-cylinder process extends an extraordinarily rich branchwork of fibres in all directions, permeating the whole granular layer with interwoven or tangled fibrils (*Kölliker*) (fig. 182, *f*). Isolated large nerve-cells with long axis-cylinder processes are also found here. Numerous medullated and non-medullated fibres of different meaning are also found in this layer.

The medullated nerves (fig. 180) of the central white substance give up their parallel or radial arrangement as soon as they enter the closer layers of the granules to form a neat network throughout the whole breadth of



the layer. They form a delicate mesh of interwoven fibres among the large cells of Purkinje in the next layer, and send not a few medullated fibres into the molecular layer, where they can be followed half-way to the surface (or the whole way, according to *Kölliker*). A great many of the medullated fibres of the granular layer, however, originate from the axis-cylinder processes of the cells of Purkinje (fig. 182, *o*). Moreover, the space between the groups of granules is filled up with fairly large round bodies which present a difficult problem in histology. Their principal constituent is certainly a network of fine closely-felted fibres. The felt-work consists of indubitable gleia-fibrils, as well as non-medullated fibres and the dendrites of the granules.

Some of these nerve-fibres, the nerve-processes of Golgi's cells, of the large cells in the granular layer, and, finally, of the granules, we have already learnt to know. In addition to these we find here collaterals of the axis-cylinder processes of Purkinje's cells, and, finally, fibres which ascend

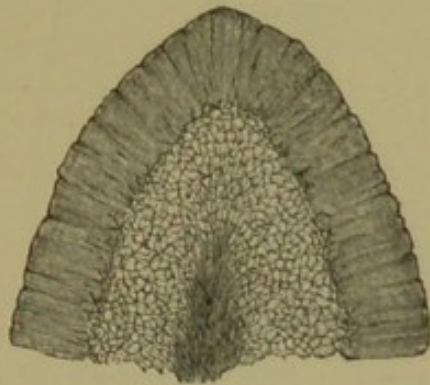


Fig. 180.—Cross-section through a lobule of the cerebellum. *Weigert's staining.* Magn. 15.

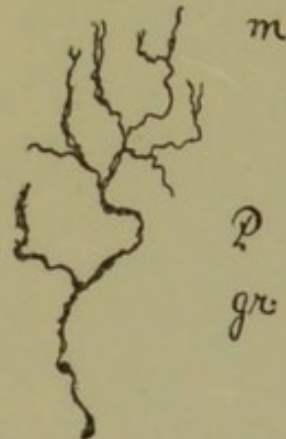


Fig. 181.—Climbing fibre from the cerebellum of a kitten.—*gr*, Granular layer; *P*, layer of large cells; *m*, molecular cells.

from the depths of the medullary centre, and break up, some in the granular layer, and some in the upper layer.

These last-mentioned fibres, wherever found, may be looked upon as cerebello-petal, and *Kölliker* classes them all together in consequence. There are other fibres which end in the granular layer itself; these divide repeatedly and bear bunches of prickles projecting in all directions, affixed either to the side or end of the fibre or to the point where it forks (mossy-fibres of *Ramón y Cajal*, fig. 182, *h*). [It happens in many preparations that in place of the mossy or 'rosette' fibres, the fibres in the granular layer, which seem from their general appearance to be the same as those usually presented as 'mossy,' give off, in place of the short arms just described, long branches which may even pass into the molecular layer. In such preparations the plexus of fibres is extremely rich, and they often appear to be in direct connection with the granules.] Others attach themselves to the under side of the Purkinje's cells; and others, again, run far into the molecular layer (figs. 181, 182, *n*). These last are irregular and knotty, and present a peculiar type of ramification. *Ramón y Cajal* named them



'climbing-fibres,' supposing that they climb like creepers up the protoplasmic processes of the cells of Purkinje.

I must, however, lay stress upon the fact that we know nothing at present of the behaviour of these non-medullated fibres in the brains of adults. The data quoted are gathered almost without exception from observations on the brains of young animals and the human embryo.

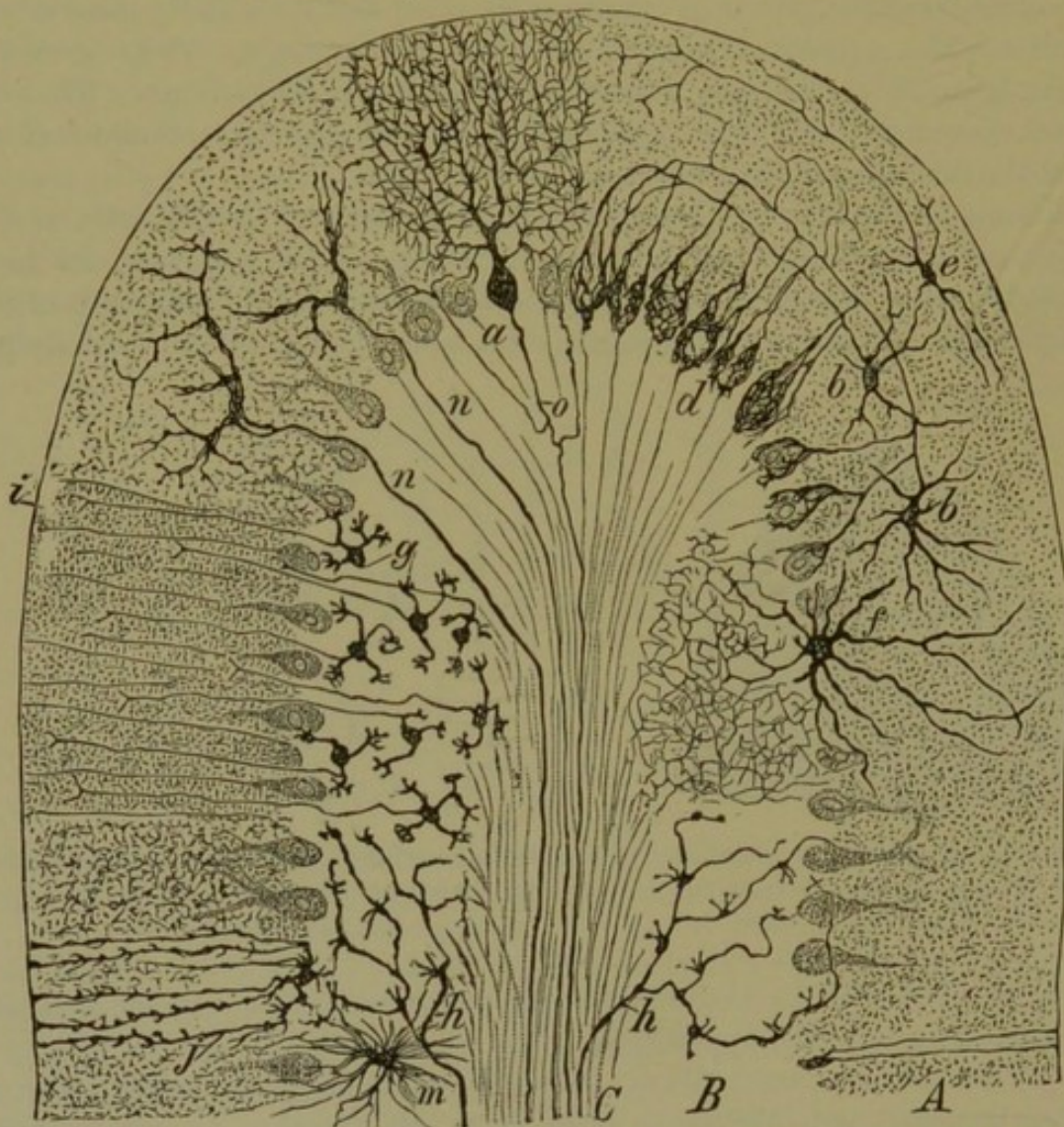


Fig. 182.—Diagrammatic section of a convolution of the cerebellum (after *Ramón y Cajal*).—*A*, Molecular layer; *B*, granular layer; *C*, medulla; *a*, cells of Purkinje; *b*, basket-cells with baskets; *d*, *e*, small cells of the molecular layer; *f*, large nerve-cells of the granular layer; *g*, granules; *h*, moss-fibres; *i*, cross-section of parallel fibres; *j*, gleia-cells of the molecular layer; *m*, gleia-cell belonging to the granular layer; *n*, climbing-fibre; *o*, axis-cylinder process of a Purkinje's cell with collaterals.

The layer of the cortex cerebelli which follows next is distinguished by its peculiar large nerve-cells. They form a sheet one-cell thick, which invests the granular layer (figs. 178, 182, and 183). The second or middle layer is, therefore, usually termed the **layer of large cells**.

The cells just mentioned (figs. 183, 184, 185), named, after their discoverer, the cells of Purkinje, have a round, somewhat flattened, shape, like a lens or a melon-seed.



The transverse diameter of these cells attains to about  $30\ \mu$ , their longitudinal diameter about  $40\ \mu$ ; it is not possible, however, to fix exactly the boundary between the cell and its peripheral process, so that the longitudinal diameter is usually stated to be somewhat greater than we have given it. Their thickness varies from  $25$  to  $30\ \mu$ .

Purkinje's cells contain a large round nucleus ( $16\ \mu$ ) with distinct nucleoli. Neither nucleus nor nucleoli possess processes as described by *Denissenko*. An exceedingly delicate cell-membrane, which is described as being continued on to the cell-processes, is not yet proved for certain, but its existence is not improbable.

The cell-body exhibits a striation which surrounds the nucleus as with a sling, and extends towards the peripheral process. It may be pointed out that these cells have not, as so many large cells have (*e.g.*, those of the spinal cord, cortex cerebri, and optic thalamus), any pigment granules, or at any rate, but very few such granules—a fact of physiological importance.

From the pole of the cell, which is turned towards the granule-layer, originates the so-called central process, broad at its base, and rapidly growing thinner, which, on account of its fineness, is soon lost amongst the granules (occasionally two such processes are present).

Only in very fortunate preparations or after the use of the silver method or the method of staining with methylene blue *intra vitam*, can the process be followed farther down. In teased preparations it tears off very easily owing to its delicacy. *Denissenko* asserts that it is surrounded with a medullary sheath, immediately after issuing from the cell.

*Golgi*, *Ramón y Cajal*, and others, have proved that numerous very fine collaterals leave the central process (fig. 180, *o*), and show a tendency to turn backwards towards the surface of the cerebellum, usually to weave themselves around other Purkinje's cells; and that the axis-cylinder process, instead of dividing dichotomously like the other processes, keeps its independence, and can be followed without diminution in thickness into the medullary substance. It is, therefore, certain that Purkinje's cells are connected with the fibres of the medullary centre by their central processes.

A thick peripheral process, which is directed towards the surface, originates from the pole of each of Purkinje's cells. It belongs, however, altogether to the layer which comes next on the outer side, the molecular layer, with which it will, therefore, be described.

The granules of the granular layer extend to a certain extent into the large-celled layer, and even into the molecular layer. The outermost of these granules are considerably larger than those which occur in the deeper parts of the granular layer. They are, almost without exception, nuclei of glia-cells, of which I shall treat later. A not inconsiderable tract of medullated fibres, which appears to envelop the granular layer, and extends both on the inner and outer sides of the cells of Purkinje, stretches parallel to the surface of the cortex.

On the whole, the large-celled layer is a very loose one [in hardened preparations it appears, owing to the shrinking of the cells of Purkinje, more open than is natural]; so that sections of the cerebellum are prone



to break across through this layer, and into it small effusions of blood are apt to be poured.

It should be noticed that at the bottom of the fissures the cells of Purkinje stand far apart, while they are closely packed together at the apices of the convolutions. The breadth of the granular layer is proportional to the number of the large cells.

It is tempting to associate this proportional relation with the development of the fissures and convolutions, but such an interdependence is not to be found. Rather is it the case that the number of Purkinje's cells is directly proportional to the extent of free surface exposed, since each cell has to provide for an equal segment of the cortical surface. Since, on the convexity, the superficial area is greater than it is in the concavity, the number of Purkinje's cells varies accordingly. The breadth of the granular layer and the number of granules depend, as already mentioned, upon the number of large nerve-cells, and certainly varies as these cells vary, although as yet the physiological connection between them is not cleared up.

The most external or **molecular layer** (finely granular or grey layer) covers the whole of the surface of the cerebellum to a uniform depth of 0.4 mm. In it the peripheral (protoplasmic) processes of Purkinje's cells are distributed (fig. 183). Each process from the peripheral pole of the cells consists, as a rule, of a short thick trunk directed straight outwards towards the surface, which soon divides into two similar chief branches disposed horizontally. From the chief branches fairly strong branches come off again at right angles and run towards the surface. All the thicker processes which originate from these branches (the case is different with the finest terminal twigs) run either parallel to the surface or else vertically to it. In the two middle fourths of the molecular layer they are almost exclusively parallel to the surface.

A single peripheral process as just pictured is only to be seen distinctly on the convexity of the convolutions. The nearer we approach the bottom of the furrows the closer does the point of division of the single stem approach to the cell, until at last at the bottom of the fissure two horizontal processes come off separately from the cell.

The thick branches (apart from the fine twigs which they give off directly) gradually dissolve into a network of excessively delicate fibres which extends as far as the free surface, and is best exhibited in its marvellous richness by Golgi's method of precipitation of silver or corrosive sublimate (fig. 184). [The ultimate twigs may be still better shown by the method of staining, first with carmine alum and then with Weigert's hæmatoxylin. They can hardly be said to taper, for the greater part of the branching is accomplished in the deeper strata of the molecular layer, and when once a terminal process is constituted it runs towards the surface, where it tends to fall back again like spray from a fountain, maintaining a uniform diameter for a considerable distance. In the shark and other animals in which numerous horizontal limbs come off from the cell, these give rise at once to radial branches which do not subsequently divide, but



traverse the whole thickness of the molecular layer with a gently undulating course.]

If sections of the cerebellum are made vertically to the surface, but in the direction of the convolutions, not, as in the preceding case, at right angles to them, a different picture is seen (figs. 179 and 185). The lateral extension of the peripheral branches is absent; their ramifications occupy a segment of the molecular layer, not much broader than the cell is thick. Hence it follows that the peripheral processes of Purkinje's cells are disposed in two dimensions only, like the stem and branches of an espalier fruit tree, not like the ramifications on all sides of a free-standing tree; a circumstance not without physiological importance.

One of the most important questions (which as yet has hardly been

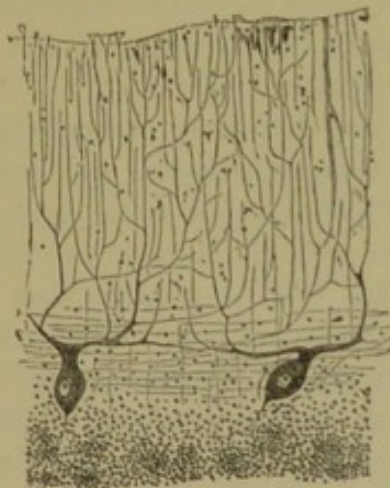


Fig. 183.—Vertical section of the cortex from the lateral surface of a cerebellar convolution. *Carmine staining. Magn. 90.*

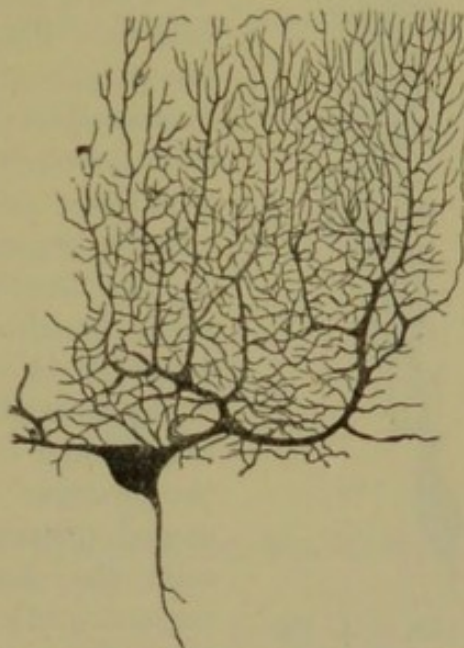


Fig. 184.—A Purkinje's cell exposed by a section vertical to the surface and at right angles to the long axis of a convolution. *Golgi's staining. Magn. 120.*

answered) is as to the ultimate fate of the finest twigs which arise from the branching of the peripheral processes of Purkinje's cells. Not seldom they have been described as ending freely on the surface.

Quantities of small granular or prickly excrescences may sometimes be seen, especially in the brains of embryos, adhering to the dendrites throughout their whole length. Many observers suppose them to be an essential part of the process. But in perfectly successful preparations of the brains of adults no such excrescences appear, only a granule here and there is seen attached to the process of an isolated cell. Without necessarily classing all such appearances as precipitates or artificial productions, we may conclude, therefore, that the majority of them do not belong to the process. [For the *translator's* views as to the nature of these thorns, see p. 444.]



It is worthy of remark that not only are coarse anastomosing branches between the cells of Purkinje wanting, but that even the very finest processes of the cells fail to unite with one another; no proper nerve network, in the strict sense of the word, is present in the molecular layer.

Numerous medium-sized and small cells lie scattered throughout the molecular layer. The larger are found in the inner half, and are characterised by the very peculiar behaviour of their axis-cylinder processes, which pass transversely, often growing thicker as they proceed above the cells of Purkinje, and give off a succession of side-branches downwards. These break up into brushes of extremely fine fibres, which

fix on or closely encircle the aforesaid cells, forming, as it were, fibre-baskets, in which the large Purkinje's cells lie. Hence these cells in the molecular layer are known as 'basket-cells.' The 'baskets' can often be seen in silver preparations, and occasionally in carmine-stained sections, but only very successful impregnation with silver exhibits clearly the sequence of cell, axis-cylinder process, and basket.

The smaller cells are dispersed throughout the whole breadth of the molecular layer, and give off dendrites in various directions, but most frequently in the same plane as the cells of Purkinje; so that in longitudinal sections (fig. 179) they often look as if the processes took rise from two poles only, and proceeded towards the centre and periphery. In these cells the nerve-process usually starts from the beginning of a protoplasmic process, and runs, for the most part, parallel to the surface. Often only a short piece of it stains (fig. 186), but in successful preparations it can be followed for a long distance. It also gives off collaterals, most of which course downwards, but do not extend as far as from the superficial cells to those of Purkinje.

Fig. 185. — A Purkinje's cell exposed by a section vertical to the surface and parallel with the long axis of a convolution. Golgi's staining.



It now only remains to recapitulate the fibres met with in the molecular layer. There are medullated fibres, coming from the deeper parts and penetrating to the middle of it—possibly to the surface; and there are processes of the basket-cells which have just been treated of in detail. On the subject of the non-medullated parallel fibres there is something to be added. We have learnt that they originate by the division of nerve-fibres which ascend from the cells of the granular layer. They are extremely abundant, so that in many sections the molecular layer looks like a bundle of fine fibres, closely packed. In cross-section they are visible as very numerous dots, filling in the spaces between the dendrites of the cells of Purkinje (fig. 182, *i*). They are present at all levels of the layer, but stain most readily in the deeper parts.



The arrangement of the gleia-scaffolding of the molecular layer deserve especial mention.

In the medullary centre and granular layer we find a considerable number of gleia-cells, rich in processes, none of which can be followed far; at least, in the granular layer. In the upper parts of the granular layer, among the cells of Purkinje, and up to the beginning of the molecular layer they are distinguished by a peculiar character. The cell-body is somewhat irregular, and the processes go off in a singular fashion, which recalls to mind the behaviour of the processes of Purkinje's cells. A thicker process (or more than one) passes inwards into the granular layer, but can seldom be followed far. From the outer side of the cell a bunch of fine parallel fibres develops, like the dendrites of the cells of Purkinje, except that the radial arrangement is even more pronounced (fig. 182, *j*). These numerous fibrils all reach the surface, where they terminate with

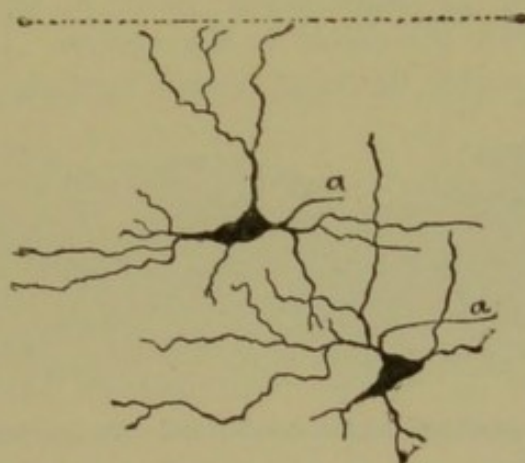


Fig. 186.—Nerve-cells from the molecular layer of the cerebellum of a kitten.—  
*a*, Axis-cylinder process.

funnel-shaped ends. The widened ends cohere firmly, and form a very delicate limiting membrane (basal membrane) beneath the pia mater. *Bergmann* long ago described this basal membrane and the radial fibres proceeding from it. It is most easily seen in a new-born child or in young animals by ordinary staining methods. More trustworthy information, however, can be gathered from silver preparations (*van Gehuchten*). Much may also be learnt from the examination of spots of softening in the cerebellum, in which the more delicate tissue-elements fall a prey, while the coarser gleia-skeleton remains intact. It is then possible to convince oneself that these radial fibres traverse the molecular layer as far as the layer of large cells, running parallel to one another without dividing.

In nuclear staining of the granular layer, as I have mentioned already, the nuclei of the gleia-cells are coloured, as well as the nervous granules.

The number and relative position of the gleia-nuclei can be best observed in sclerotic processes in the cortex cerebelli. At the transition points between diseased and normal tissue the cross-section clearly shows that a numerical increase of gleia-nuclei is out of the question.

It also shows that all the nervous constituents of the cortex have



come to grief, while, on the other hand, in nuclear-stained preparations we find the nuclei of the gleia-cells everywhere intact (fig. 187). Throughout the medullary centre and granular layer the granules are scattered; only on the outer periphery of the latter do we find them packed in a close layer, which goes through the convolutions as a neat regular band from 60 to 80  $\mu$  in breadth. Most of the radial fibres which pass to the surface take origin from the cells of this band. In the molecular layer, again, the gleia-nuclei are scattered at wide intervals, sometimes more closely set in the middle, but diminishing in number again, until in the outer parts they become particularly scarce. A cross-section of this kind gives us the best idea we can gain of certain matters connected with the gleia-cells.

In the molecular layer, the dendrites of Purkinje's cells, the radial gleia-fibres, the climbing fibres, and, finally, the larger branches of the blood-vessels from the pia-mater which pierce it, all run in the same direction, straight from the centre to the surface. It is therefore easy to understand that under the most varied methods of treatment this

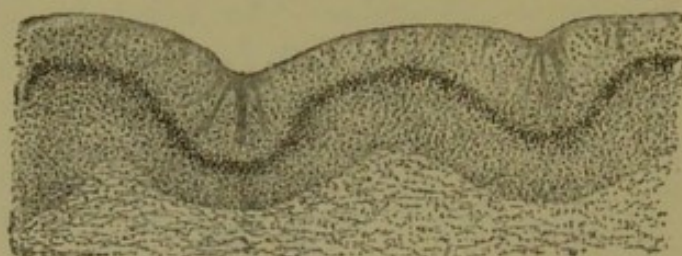


Fig. 187.—Sclerosis of the cerebellum. *Nuclear staining.*

layer exhibits a radial striation. It is known, in consequence, as the radial layer.

In all parts of the cerebellum the cortex exhibits the structure just described; no local differentiae are yet known; we may well conclude from this circumstance that over the whole of the cerebellum the function is the same.

A striking similarity of structure is exhibited by the cortex cerebelli throughout the whole vertebrate series. It is not to be denied that a certain harmony between size of the animal and the diameter of the cells of the cerebellum obtains amongst mammals. This parallelism affects the cells of Purkinje in the first place, but the granules also to a certain extent.

Apart from these variations in size, the cortex cerebelli presents in mammals a remarkable uniformity in structure; but the complexity of the branching system of Purkinje's cells is nowhere else so great as it is in Man; this character is most conspicuous if the human cerebellum is compared with that of small mammals, especially rodents.

The connective tissue is more compact in the cerebellum of many animals than it is in Man. In the cat the basal membrane with its radial fibres can be easily seen, and the fibres can be followed for a long distance into the molecular layer.



The structure of the cerebellum of birds closely coincides with that seen in mammals. *Tenchini* and *Staurenghi* assert that the large-celled layer is very strongly developed in the eagle. Wider differences are met with when we come to other classes. In reptiles, amphibia, and fishes the large-celled layer is especially broad, owing chiefly to the numerous medullated fibres lying parallel to the surface. In consequence, Purkinje's cells are not arranged in a single sheet, but lie many cells thick. Moreover, the cells just named do not present in the lower three classes of vertebrates the round form characteristic of birds and mammals; they rather tend to assume a more or less fusiform or triangular shape. Their peripheral processes ramify in a somewhat different manner to those of birds and mammals. After branching a few times they run directly towards the surface, giving off only a few lateral branches which cannot be followed farther. Near the surface the connective tissue grows so soft and loose that this part of the cortex often looks like a delicate lace-work.

A further peculiarity of the cerebellum of many lower animals consists in the reduction of the central medullary substance to a minimum; sometimes it is completely wanting in places, all the medullated fibres lying in the granular layer. In plagiostome fishes the main body of the medullated fibres lie beneath the cells of Purkinje only in the outer part of the granular layer; so that the medullary substance and the granular layer appear to have exchanged places.

The **histological development** of the cerebellum is fairly well worked out. In Man it consists at first of a quantity of round granules in which, about the middle period of embryonal life, a band free from granules makes its appearance, lying parallel to the surface, between it and the granular layer [but leaving a layer of granules beneath the pia mater. This layer is a conspicuous object in sections of cerebella from new-born animals]. This band is the developing molecular layer which even now presents a considerable likeness to the molecular layer in the adult. At the same time, or even a little earlier, the medullary centre, formed at first, of course, of non-medullated fibres only, advances towards the surface. At the end of the sixth month the cells of Purkinje can be usually, but not always, recognised along the inner border of the molecular layer. At birth, nerve-cells are usually very visible in carmine preparations (fig. 188), although their processes are as yet but slightly branched.

Although the breadth of the molecular layer slowly increases, that of the outer granular layer remains, even up to birth, about the same; only then does it begin to dwindle, and, finally, at varying periods of development disappear.

At birth, and in Man shortly before birth, the outer granular layer can be divided into two nearly equally broad strata (fig. 188). It is probable that all the superficial cells either are transformed into glia-cells or atrophy. In the corresponding stages of development we find bipolar fusiform cells disposed in a horizontal layer, parallel to the surface; in the deeper, exterior granular layer. In silver preparations we can



see that these fusiform cells undergo a curious transformation into granules of the granular layer. The two horizontal processes lengthen, and so form parallel fibres, while the cell-body sinks through the molecular layer, down to the granular layer, maintaining its connection with the parallel fibres which went off from it originally by means of a thin nerve-thread which lengthens as the cell travels down. Finally, as it enters the granular layer, the cell puts forth the protoplasmic processes (*Ramón y Cajal, Lugaro, Schaper*).

It is not to be supposed that this mode of development is common to all the granules of the granular layer; some, no doubt, develop *in situ*.

Very few medullated fibres are found in the granular layer at birth (*A. Meyer*).

It has been already mentioned that the nerve-cells of the corpus dentatum cerebelli are among the earliest to be developed. At the sixth

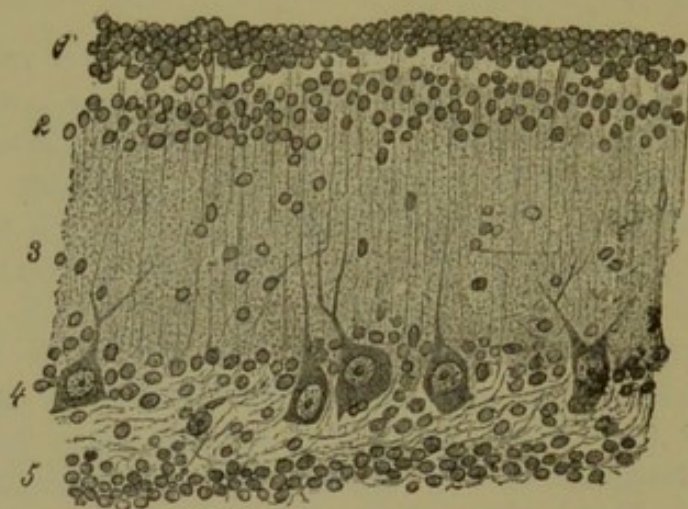


Fig. 188.—Cortex cerebelli at birth. *Carminic staining*.—1, Peripheral stratum of outer granular layer; 2, inner stratum of the same; 3, molecular layer; 4, layer of Purkinje's cells; 5, inner granular layer.

month they are marked out by their striking development, but hitherto we have been able to make no use of this circumstance for the explanation of their function.

[The cerebellum certainly offers the most favourable opportunity for studying the structure of the cortex, and determining the plan of formation of this tissue, for although, at first sight, its cortex appears unlike that of the cerebrum, there is no sufficient reason for thinking that the two are fundamentally dissimilar. In the cortex of all parts of the brain are found large nerve-cells and granules in varying proportion. The nerve-cells provide for the nutrition of descending fibres. The granules are in all probability small nerve-cells in connection with non-medullated processes, into which the ascending fibres break up on reaching the grey matter. Such is the *translator's* view, based upon the study of the cerebellum. The medullary substance of this organ contains more fibres than are needed to supply one to each cell of Purkinje. Amongst the granules are clumps of matrix containing non-medullated



fibres. Non-medullated fibres are seen to break through into the molecular layer between Purkinje's cells, while the ultimate processes of these cells curve backwards towards the granular layer. There is no reason to suppose that the cells of Purkinje differ from the large cells of the cortex cerebri in not giving rise to efferent fibres. On the contrary, pathological observations point to such a connection, since they are not affected by ascending degenerations. Far as such a theory may be from giving a complete explanation of cortex formation, our conception of this tissue is simplified by looking upon it as a field in which impressions received along the ascending fibres and their fibrils with which granules are connected, are collected after their distribution through the cortex by the processes of the large cells for transmission from the cerebellum to the cortex cerebri, from the cortex cerebri to the grey matter which surrounds the central canal.]

**4. Blood-Vessels of the Cerebellum.**—In Man the cerebellum is chiefly supplied with blood from the vertebral artery.

Three arteries reach it on either side.

(1) *Arteria cerebelli inferior posterior*, which comes off as a rule from the uppermost portion of the vertebral artery, but sometimes from the commencement of the basilar artery; (2) *arteria cerebelli inferior anterior* from the basilar; and (3) *arteria cerebelli superior* from the front of the basilar shortly before it splits into the two posterior cerebral arteries. The superior cerebellar artery is very constant; whereas the other two are often wanting, though usually on one side only. The anterior inferior cerebellar artery has the smallest calibre of the three. All three leave the main artery at right angles. Within the pia mater the vessels divide repeatedly, and only small delicate branches enter the substance of the cerebellum. From the anterior inferior cerebellar artery a larger branch comes off, however, and is directed towards the corpus dentatum, through the hilum of which it enters the medullary substance, *arteria corporis dentati*. The larger veins in the interior of the medullary substance of the corpus dentatum have been already mentioned.

The capillary network of the cerebellar cortex shows certain peculiarities corresponding with the stratification of the nerve-elements.

The arteries and veins enter the molecular layer vertically, and continue in this direction as far as the cells of Purkinje. There the capillary vessels form an abundant close network with oval meshes, the long axes of the ovals being arranged radially as it appears. The upper layer of the cortex contains no capillary network (*Oegg*). In the granular layer we find a capillary network of rather narrow mesh. On passing on into the medullary substance, the meshes of the network become wider, and are elongated in the direction of the fibres. Larger vessels, both arteries and veins, attract attention in the zone of the cells of Purkinje; they run almost parallel to the surface, and are devoted to the nourishment of the large cells. At birth the cerebellum contains comparatively few, but wide, vessels; already, however, the peculiarities characteristic of their distribution are recognisable.

**5. Pathological Changes in the Cerebellum.**—On the whole the



anatomical changes in this organ due to disease are similar to those which occur in the rest of the brain. In this place we shall only point out such as are characteristic. But it is worthy of note that in the cerebellum many pathological processes do not merely assume a distinctive local character, but present specific peculiarities which force us to infer, for it histological conditions differing in very essential points from those which obtain in other parts of the brain. It is a conspicuous example of the way in which pathological changes in the tissue often give hints for our guidance in the study of certain normal conditions.

Small clumps of grey matter resembling cortex (fig. 189), the little heterotopia mentioned on p. 392, are among the commonest structural

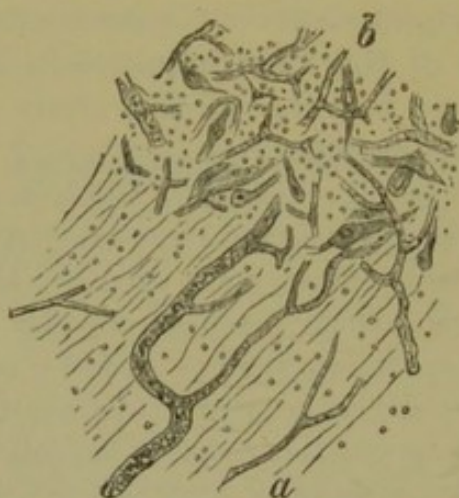


Fig. 189.—Section through a small heterotopia in the medullary substance of the cerebellum. *Magn.* 40.—*a*, Medullary substance; *b*, the grey patch.

defects of the cerebellum. A similar state of arrested development in larger masses, producing a fallacious appearance of atrophy of the cerebellum, is rare (*P. Ernest*).

ATROPHY of the cerebellum has been often described; a distinction must be made, however, between a strikingly diminutive, but otherwise normal, cerebellum and a cerebellum in which the falling-off in size is associated with sclerosis of its tissue.

CONGENITAL ATROPHY belongs to the first class only; the latter class of atrophies are, of course, acquired.

In these cases, which involve very marked changes in the tissue of the cerebellum, the cortex and medullary centre may be affected equally, or the process may spread inwards from the cortex; or, finally, the medullary substance may be first sclerosed, and the changes in the cortex may be secondary and inconsiderable. This last state of things is the rarest. (*M. Arndt*.)

Where one hemisphere of the cerebellum is atrophic the brachium conjunctivum and the contra-lateral red nucleus are usually diminished in size, as is also the opposite cerebral hemisphere. Atrophy of the opposite olive is almost always associated therewith. On the other hand, in the case of a defect of long standing in the cortex of the gyri centrales (the



posterior gyrus, more especially), *Flechsig* and *Hösel* found the nucleus dentatus shrunken and atrophied, and the brachium conjunctivum reduced by one third, on the right side; while the red nucleus on the left side was considerably smaller. It is not, however, safe to generalise from these observations.

*A. Meyer* is said to have proved that a considerable reduction of the medullary fibres in the cortex cerebelli takes place in certain forms of mental disease, such as senile and paralytic dementia. *Jellinek* found a similar state of things in tabes.

SENILE ATROPHY brings about no conspicuous changes in the cerebellum. Even the amyloid bodies which collect in immense numbers in various parts of the central nervous system in old age, are less numerous here. They are found chiefly on the surface, but a few are scattered throughout the whole breadth of the molecular layer. They can even be followed at still wider intervals down among the medullated fibres.

SCLEROSIS of the cerebellum usually attacks the posterior lobe, and leads to the complete destruction of all nervous organs. We can then observe the peculiar behaviour of the granules described on p. 407. A growth of close tissue unites in places the near surfaces of neighbouring convolutions, leaving cyst-like gaps between. Scattered amyloid bodies are dispersed in the sclerosed convolutions. The medullary centre is transformed into a mass of perforated tissue, from which the medullated fibres have completely disappeared.

EMBOLISM of a cerebellar artery is very rare. Owing to the three arteries of the cerebellum coming off at right angles from a much more considerable trunk, it will be easily understood that the embolus, as a rule, floats away in the basilar artery, and is not stopped until it reaches the posterior cerebral artery.

Large APOPLEXIES of the cerebellar substance are much more rare, too, than in other parts of the brain. This is due to the fact that in the cerebellum hardly any besides the very smallest arteries occur; the only artery of somewhat larger size, *arteria corporis dentati*, is consequently the commonest source of extended bleeding into the cerebellum.

CAPILLARY HEMORRHAGES are sometimes met with, especially in the cortex of the cerebellum. In these cases one can usually see that the little effusion of blood has spread out horizontally in the layer of Purkinje's cells where it found the least resistance.

CALCIFICATION OF THE VESSELS is not uncommon, especially in the capillary network. A striking feature of these chalky deposits is that they are always most distinct in the granular layer and hardly ever extend to the molecular layer (*cf.* p. 178). The larger calcifications sometimes met with in the cerebellum probably start, in many cases, from the vessels.

Amongst TUMOURS found in the cerebellum the first place is occupied by tubercle. It occurs much more often in the cerebellum proportionally to its size, than in any other part of the brain. Often several masses of tubercle are present at the same time; usually they originate in the pia mater and are sharply marked off from the surrounding brain-substance.



They may be so large that a whole hemisphere, or even more, of the cerebellum is changed into a tuberculous mass. Glioma and carcinoma also belong to the more frequently occurring tumours. Passing over certain other new formations (such as fibromas, sarcomas, etc.) we will notice some which are interesting on account of their rarity, *e.g.* dermoid cysts (*Clairat, Irvine, Heimpel*), osteomata (*Ebstein*) and echinococci which have penetrated from the fourth ventricle.

INFLAMMATORY PROCESSES often affect the cerebellum and its meninges. Purulent meningitis may be of traumatic origin, but it is usually secondary to disease of other spots on the surface of the brain or on surrounding bones (*e.g.*, temporal bone).

Inflammation of the substance of the cerebellum produces necrosis in some cases, but more commonly local softening of the tissue—cysts and abscesses—which are relatively very common in this organ. Sometimes a

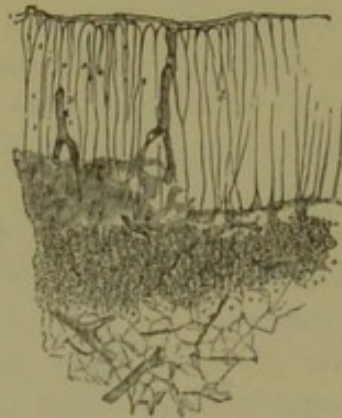


Fig. 190.—Vertical section of the cortex cerebelli from a case of encephalitis in which the connective-tissue elements of the cortex were not destroyed. The radial fibres of the molecular layer are distinct; so, too, are the holes out of which Purkinje-cells have fallen. Some medullated fibres remain in the connective-tissue framework between the granular layer and the medullary substance. *Weigert's stain. Magn. 60.*

whole hemisphere is turned into a cyst or an abscess-sac. Diverticula of the fourth ventricle may develop into cysts within the substance of the cerebellum; sometimes they still communicate with the cavity of the ventricle.

In consequence of circumscribed chronic encephalitis the nervous constituents of the cerebellar cortex and underlying white matter may come to grief almost completely, only the connective-tissue framework remaining intact; the preparation looking as if it had been successfully macerated. Such specimens show us the arrangement of the gleia in the cerebellum more plainly than any others (fig. 190). Isolated intact nerve-fibres are, however, to be found in the nuclear layer and in the central medullary substance after all the nerve-cells have disappeared (*Hess*), the spaces in which the cells of Purkinje used to lie being still recognisable.

*Secondary degeneration* may be followed far into the medullary substance after destruction of portions of the cerebellar cortex (*Borgherini*); especially when the lesion of the cortex is quite a small one. A number of well-



preserved fibres may also be found coming out of the diseased piece of cortex amongst the fibres of this degenerated bundle. From this it follows that of the fibres connected with the cerebellum some must have their trophic centres within this organ, and a smaller number (centripetal fibres) must have their trophic centres elsewhere.

Some stress must be laid upon the circumstance that the cells of Purkinje in the cerebellum are, on the whole, less liable to degeneration than (for example) those of the cortex cerebri. Fatty and pigmentary degeneration very rarely occurs in them; varicose hypertrophy of the central process was observed by *Hadlich*. *Roth* has described calcification of the cells of Purkinje and their peripheral processes.

There is very little to be said about pathological changes in the **pedunculi cerebelli** and the **pons**.

In atrophy of one of the hemispheres of the cerebellum, degeneration of the corresponding brachium pontis and the same side of the pons is especially noticeable. Changes in the brachia conjunctiva are also found after extirpation of one of the hemispheres, and the existence of uncrossed fibres can then be demonstrated (*Marchi*). Atrophy of the nuclei of the pons is found associated with secondary degeneration of certain parts, *e.g.* the lateral bundle of the crus cerebri.

Small aneurysms are common in the arteries of the pons, and hence apoplexies of this region are not rare. Patches of softening and tumours (especially tubercle) have been repeatedly seen. Aneurysm of the basilar artery must have a lasting effect owing to its pressure on the pons.

The pons is a favourite spot for sclerotic lesions in disseminated sclerosis.

The pathology of the brachia pontis is the same as that of the pons. Independent isolated disease of the other peduncles of the cerebellum is rare.

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## D. THE CEREBRUM.

In treating of the great brain we will first describe the central grey masses which it contains, their intimate structure and connections with other parts of the brain; then we will attempt to unravel as far as possible the separate tracts which occupy its medullary substance, and only when this has been done shall we devote a more detailed consideration to the minute structure of the cortex cerebri.

### I. THE GANGLIA OF THE GREAT BRAIN.

(1.) **Thalamus opticus.**—On both free surfaces of the thalamus, mesial as well as dorsal, a superficial stratum covering the grey matter is



to be recognised apart from the ependyma of the ventricle. On the mesial surface this layer is formed of grey matter, the central grey substance of the ventricle. On the dorsal surface it consists of tracts of white fibres, stratum zonale.

The central grey matter lining the thalamus is a continuation of the

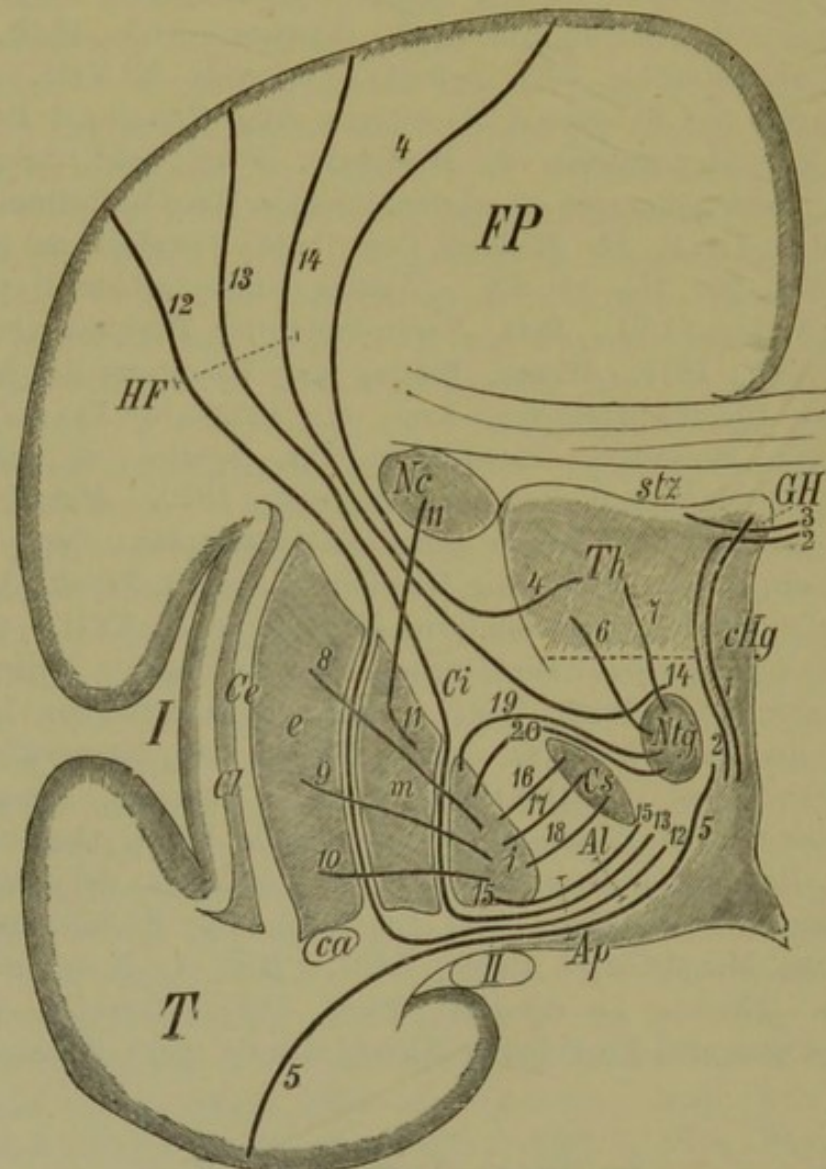


Fig. 191.—Diagrammatic frontal section through the great brain.—*FP*, Frontal parietal lobe; *T*, temporal lobe; *I*, island of Reil; *II*, tractus opticus; *HF*, fibres from the tegment; *Nc*, nucleus caudatus; *Th*, thalamus opticus; *GH*, ganglion habenulæ; *cHg*, central grey matter; *Ce*, capsula externa; *Ntg*, nucleus tegmenti; *Cs*, corpus subthalamicum; *i*, *m*, *e*, the three segments of the nucleus lenticularis; *Ci*, capsula interna; *Cl*, claustrum; *ca*, anterior commissure; *Ap*, ansa peduncularis; *Al*, ansa lenticularis; *Stz*, stratum zonale; 1 to 20, tracts of fibres referred to in the text.

grey matter which surrounds the aqueduct and terminates in front in the lining of the infundibulum. Basewards it forms the floor of the third ventricle, or grey commissure of the floor, in which the chiasma nervorum opticorum is embedded (fig. 15).

The central gray lining is not everywhere distinguishable from the true thalamic substance. It consists of a gleial ground substance similar



to that found in the masses of grey substance, and containing nerve-cells and fibres, the further connections of which are not known.

We have learnt to distinguish a number of subdivisions in the optic thalamus, the anterior nucleus, mesial nucleus, centre médian, and pulvinar. To these *Monakow* adds the posterior nucleus, on the ventral side of the pulvinar, wedged in between the corpus geniculatum externum and internum. He also regards the ventral nucleus (bowl-shaped or crescentic nucleus, nucleus arcuatus) as distinct from the rest of the thalamus.

The mesial (vertical) surfaces of the thalamus grow together at one circumscribed point, forming the middle commissure.

The **middle commissure** (commissura mollis) (figs. 15 and 152) is a part of the central grey lining, and contains a considerable number of nerve-fibres, not united into bundles, some of which run laterally into the thalamus, others bend over so as to course in various directions within the central grey lining parallel to the wall of the ventricle. A few of the fibres are continued into the inferior (inner) peduncle of the thalamus (*Fritsch, Holländer*). *Villier* denies that any nerve-fibres cross the middle line in the middle commissure. Only a few isolated nerve-cells are found in it, a sprinkling from the thalamus; together with a fair number of gleia-cells.

In mammals the greater part of the two mesial surfaces of the thalami is united, and the middle commissure is consequently much larger than in Man; but the number of medullated fibres which pass that way from one hemisphere to the other is nevertheless very small. No particular physiological importance can be attached to the middle commissure.

The **stria medullaris thalami (habenula)** is a bundle of medullated fibres which in Man runs along the junction of the vertical and horizontal surfaces of the thalamus. It originates from the ganglion habenula on either side (or, as *Kölliker* thinks, ends in the contra-lateral ganglion). In front it splits up into several branches, one of which extends to the pillar of the fornix, curves up against, and so passes backwards towards the cornu Ammonis; another reaches the base of the brain and ends above the lamina perforata anterior in a group of cells known as the nucleus of the basal longitudinal bundle (*Lotheisen*).

The **ganglion habenulæ** (figs. 12, 15, 19; and 191, *GH*) is a group of small nerve-cells, not well-defined in Man and the Primates. In most mammals, on the other hand, it attains a very considerable size, and becomes quite massive in low vertebrates—amphibious animals and reptiles. Fibres from the pedunculus conarii enter this ganglion. Other sets of fibres from the nerve-bundle just mentioned probably merely traverse or pass over the ganglion.

A large column of fibres, usually visible to the naked eye, which leaves the ganglion habenulæ and passes towards the base of the brain with a slight convexity outwards, deserves especial notice. It runs between the central grey lining and the substance of the thalamus itself, and appears to end, as seen in frontal sections, on the mesial side of the red nucleus



(fig. 191, 1; fasciculus retroflexus, Meynert's bundle). The greater part of this bundle extends, after crossing (*Edinger*), to a group of nerve-cells (ganglion interpedunculare) which lies in the hinder part of the substantia perforata posterior, and is very distinct in certain animals—rodents and bats, for example. The cells corresponding to this ganglion do not form a well-defined ganglion, but are disposed in a diffuse manner just in front of the commencement of the pons, in the middle line of the most basal part of the tegmental region. But a not inconsiderable part of this bundle can be followed farther spinewards into the tegmental region. *Mendel* observed atrophy of the ganglion habenulæ in the rabbit as a consequence of iridectomy, and concludes that the pupillar fibres of the optic nerve end there. Others, among whom *Edinger* is foremost, connect it with the olfactory apparatus.

The fibres of the fasciculus retroflexus degenerate after destruction of the ganglion habenulæ, from which we must infer that they take rise from it and terminate in the ganglion interpedunculare. The axis-cylinders which take origin from the cells of the latter seem to turn spinewards in the tegmental region.

A part of the pedunculus conarii crosses over Meynert's bundle and joins it on its outer side. The two then extend basewards together, 2. In carmine preparations fibres of two kinds can be clearly distinguished in the fasciculus retroflexus; the coarser conspicuously white, the finer of a curious red colour. The former probably course spinewards, across the ganglion interpedunculare.

*Darkschewitsch* has proved that the peduncles of the pineal gland contain, in addition, fibres which form a crossed connection between the tractus opticus and the oculomotor nucleus (*cf.* p. 346).

The **stratum zonale** forms a white coat not quite one millimeter thick on the upper surface of the thalamus; it is composed of medullated fibres running for the most part in a sagittal direction. The following sets of fibres take part in its formation.

(1) Fibres from the lateral root of the optic tract, which, passing superficially to the corpus geniculatum laterale, spread out over the thalamus.

(2) Fibres which extend out of the occipital lobes, and, perhaps, the temporal lobes also, in the sagittal medullary strata, coursing forwards (or backwards) to reach the surface of the pulvinar.

(3) Fibres out of the peduncle of the thalamus, to be described later on.

Most fibres of the stratum zonale penetrate into the substance of the thalamus.

The lateral boundary of the grey mass of the thalamus is not everywhere sharply defined. Quantities of fibres stream into the thalamus on this side, so that grey and white matter are mixed up (stratum reticulatum). In animals the lateral surface of the stratum reticulatum is noticeable for its richness in medullated fibres (lamina medullaris externa).

So far as the bundles of fibres which stream into the thalamus



originate in the cortex cerebri, they take part in forming the **corona radiata of the thalamus**, of which the following are the principal constituents:—

(1) Fibres from the frontal lobes, which pass to the thalamus in a sagittal direction between the nucleus caudatus and nucleus lenticularis in the anterior portion of the internal capsule, anterior peduncle of the thalamus (fig. 191, 4).

A bundle, very inconsiderable in size in Man, comes from the cortex of the lobus olfactorius (*cf.* p. 332). It separates from the tract of fibres destined for the anterior commissure, and extending farther backwards enters the front part of the optic thalamus.

(2) Fibres from the parietal lobe which, piercing the posterior part of the internal capsule in thin bundles, sink into the lateral surface of the thalamus.

(3) Great bundles of fibres for the occipital lobe, and to a certain extent the temporal lobe also, which pass backwards in a sagittal medullary stratum to the thalamus (optic radiations of Gratiolet, posterior peduncle of the thalamus). A few of these fibres may come from the stratum zonale.

(4) Fibres which pass, partly through the anterior limb of the capsule and partly beneath the inner capsule, from the nucleus caudatus and putamen (which represent parts homologous with the cortex) to the 'tween-brain, more especially to the thalamus (Edinger's basal fore-brain bundle, radiatio strio-thalamica); these fibres myelinate early (in the eighth month).

(5) By the inferior peduncle (stalk) of the thalamus, fibres are conducted from the temporal lobe itself, beneath the nucleus lenticularis, to the base of the thalamus (fig. 152, *ust*). A part of these fibres reaches the surface of the thalamus and helps to form the stratum zonale; by *Wernicke* it is termed the inner peduncle of the thalamus. Another part streams directly into the substance of the thalamus. The term 'inferior' peduncle, and still more the term 'internal' peduncle, is used very loosely by many authors. *Brissaud* terms the part which comes from the temporal lobe 'bandelette sous-optique.'

If the tractus opticus is dissected away from the base of the brain the crus cerebri is exposed as it disappears in the substance of the hemisphere. The structures on the base of the brain which invest the crus as it enters the hemisphere—sling themselves around it, as one might say—are termed collectively the ansa peduncularis, *Ap* (substantia innominata, fig. 191). The inferior stalk of the thalamus is an important constituent of the ansa peduncularis. Another constituent is the ansa lenticularis.

We shall see later on that all the bundles which enter into the formation of the ansa peduncularis have in their disposition certain points in common. They all agree in passing medianwards out of the region which lies on the ventral side of the nucleus lenticularis, and, therefore, as we learn from frontal sections (figs. 152, 191) in



arching round the ventral part of the internal capsule, as the direct continuation of the now covered-up pes pedunculi cerebri is called. They closely invest this structure before they separate to pass in various directions beneath the thalamus.

It has been already mentioned that fibres out of the lateral root of the optic tract, passing under the corpus geniculatum laterale, stream in a brush into the pulvinar. Connections of the thalamus with the anterior quadrigeminal and lateral geniculate bodies exist for certain; its connections with the nuclei lenticularis et caudatus have already been discussed. A part of the posterior commissure is also connected with the thalamus. We also know that the bundle of Vicq d'Azyr courses from the corpus mammillare to the anterior nucleus of the thalamus. The greater part of the lateral fillet ends in the thalamus (*cf.* p. 307); a point of the highest importance. Lastly, the thalamus is united with the tegment and the spinal cord in manifold ways not yet clearly understood. The fibres of the laminae medullares seem especially to establish these connections, of which the most important and best known are with the red nucleus; 6, 7 (*fig.* 191 *cf.* p. 292) and the fillet. By many (*Meynert, Wernicke, etc.*) the posterior commissure is looked upon as the commencement of the crossed tegmental connection of the thalamus.

The thalamus is thus in connection with almost all parts of the cortex cerebri; with frontal, parietal, and occipital lobes through the internal capsule; with the temporal lobe through the ansa peduncularis; with the nervus opticus, corpus mammillare, and with the spinal cord and the tegmental region of the medulla oblongata through the mesial fillet and posterior commissure; lastly, with the cerebellum by the red nucleus and brachium conjunctivum. Many other connections besides those enumerated above certainly exist.

We must picture to ourselves the optic tracts, as well as all other groups of fibres which connect the thalamus with parts of the brain other than the cortex or its homologues, as finding their terminus, for the most part, in the thalamus; and must look upon most of those which take rise in it as what we may call thalamo-cortical tracts. (*Kölliker*, on the contrary, is of opinion that most of the fibres of the corona radiata of the thalamus end in it.) And it is certainly demonstrable that to each separate division of the thalamus a corresponding area of limited extent is assigned in the convolutions (*Monakow*).

With regard to the **minute structure** of the thalamus, it may be said that the nucleus externus is very rich in white fibres, hence its light colour. The nerve-cells of the thalamus are for the most part fairly large and strongly pigmented. Smaller cells, usually spindle-shaped, occur, chiefly in the external nucleus, and particularly large cells are met with in some parts, especially in the ventral divisions. *Kölliker* distinguishes two kinds of cells in the thalamus: 1, radiate cells, which are elongated in general outline and have long dendrites; and 2,



bushy cells, roundish in shape, with short dendrites which break up into exceedingly rich brush-like ramifications.

The **physiological meaning** of the thalamus can be only imperfectly gathered from its anatomical relations. That its functions lie chiefly in the region of sensibility may be inferred from the fact that it is the most important terminal station of the lateral fillet. Probably the functions with which we have to do here are diverse and somewhat complicated; though they may all be construed as 'reflex' in the widest sense of the word. We are apparently justified, therefore, in assuming that in one aspect the thalamus should be regarded as a reflex centre for movements expressive of emotion brought about by the agency of the facial nerve and the other motor nerves of the brain and cord.

(2.) **Nuclei Lenticularis et Caudatus.**—The nucleus caudatus and the external segment of the nucleus lenticularis (putamen), which are united to one another in a number of ways, may be considered as modified portions of the cortex cerebri.

A thickening is formed in the floor of the anterior cerebral vesicle which constitutes the rudiment of the above-named grey masses; even in the completely developed brain the putamen is continuous with the grey covering of the substantia perforata, which is undoubtedly homologous with the rest of the cortex.

Apart from these genetical connections with the cortex, *Wernicke* has proved conclusively that fibres which are the homologues of the corona radiata come off from the nucleus caudatus and putamen, and enter, for the most part, the two inner segments of the nucleus lenticularis (globus pallidus), making use of it as an intermediate station (8, 9, 10, 11, fig. 191).

The fibres coming out of the putamen collect on its mesial border into distinct coarse bundles which, traversing the lamina medullaris nuclei lenticularis lateralis, reach the globus pallidus. Corresponding bundles from the nucleus caudatus, crossing the anterior division of the internal capsule, extend both to the lateral lamella and also to the second segment of the nucleus lenticularis, where they agree with the fibres from the putamen in assuming a mesial direction (11); it is these fibres which give a radial striation to the globus pallidus when seen in frontal section.

The two laminæ medullares, to which a third plate of white fibres is sometimes added owing to the splitting of the inner segment of the nucleus lenticularis into two, consist, as far as we can judge, of fibres which come, for the most part, out of the nucleus caudatus and putamen, but course basewards, not taking part in producing the radial striation of the globus pallidus.

According to *Edinger*, other bundles of fibres which come from the cortex of the parietal lobe, and receive their medullary sheaths at an earlier period than the rest of the fibres of the great brain, also take part in the formation of the laminæ medullares (12, 13). These fibres



are called tegmental by *Edinger*, but he reckons amongst them still other fibres (14) which do not enter the nucleus lenticularis, but pass spinewards beneath the thalamus and above the red nucleus to join the fillet.

Lastly, fibres are found which come out of the grey substance of the middle segment of the nucleus lenticularis and bend round into the internal lamina medullaris; for the sake of simplicity they are omitted from fig. 191.

All the fibres which run basewards in the medullary laminae turn medianwards beneath the globus pallidus, from which they receive additions (15), and there unite with a part of the basal fore-brain bundle (p. 421). In this way they form the ansa lenticularis, *Al* (better, ansa nuclei lenticularis), another constituent of the ansa peduncularis.

The internal capsule lies mesio-dorsally to the nucleus lenticularis, separating it from the nucleus caudatus and the thalamus, or rather from the regio subthalamica (stratum intermedium).

The ansa nuclei lenticularis as it traverses the most mesial and basal parts of the internal capsule comes into this regio subthalamica; farther back it lies beneath the red nucleus on the base of the brain, near the middle line; beyond this it cannot be followed with any certainty. Since the posterior longitudinal bundle increases quickly in the neighbourhood of the ansa lenticularis, *Wernicke* is of opinion that it is connected with it by means of fibres ascending in the raphe. The fibres of the posterior longitudinal bundle exceed those of the ansa peduncularis in calibre, and hence such a connection is only possible on the supposition that nerve-cells are intercalated between the two sets of fibres. *Bechterew* and *Flechsig* are of opinion that there is no connection between the ansa peduncularis and posterior longitudinal bundle. By these authors the ansa peduncularis is considered as prolonged down through the central tegmental tract as far as the inferior olive (*cf.* p. 315). It was on this ground that we described the nucleus lenticularis as connected with the inferior olive of the same side, and, by this means, with the cerebellar hemisphere of the opposite side.

When it is considered that the posterior longitudinal bundle is medullated much earlier than the ansa lenticularis, it will be understood that a direct connection between the two is impossible.

*Edinger* supposes that a considerable portion of the ansa peduncularis enters the corpus subthamicum.

Still other fibres enter the regio subthalamica from the nucleus lenticularis, all, it is unnecessary to add, traversing the internal capsule.

We have already seen the corpus subthamicum, *Cs* (nucleus of Luys), on the dorsal side of the internal capsule in this region, and, more in the mid-brain, above the pes pedunculi cerebri, the substantia nigra *Soemmeringi*. Fibres from the internal segment of the nucleus lenticularis enter both ganglionic masses (16, 17, 18). They are fibres which



can be seen in frontal sections coming from the dorso-mesial surface of the nucleus lenticularis and traversing the internal capsule. By a mistake easy to understand they have been looked upon as a root of the optic nerve from the nucleus of Luys. They give the inner capsule the characteristic cloven appearance noticeable in front sections. *Monakow* supposes that these fibres take rise from the cells of the corpus subthalamicum and end in the nuclei lenticularis and caudatus. The uppermost (most dorsal, 19, 20) of these fibres do not enter the corpus subthalamicum itself, but collect, after passing the internal capsule, into a compact bundle which constitutes the dorsal portion of the capsule of the corpus subthalamicum and enters the red nucleus according to *Wernicke* (tegmental bundle from the nucleus lenticularis). This connection with the red nucleus is represented in fig. 191; but must, nevertheless, be considered very doubtful.

The ansa nuclei lenticularis and the inferior peduncle of the optic thalamus together make up the ansa peduncularis (*cf.* p. 421). According to *Meynert* a system of fibres is supposed to push its way between these two systems (posterior medullary lamina of the tegment).

The external capsule, if it sends any fibres into the nucleus lenticularis, sends to it but inconsiderable tracts; hence in hardened preparations it is very easy to peel off the external capsule from the nucleus lenticularis; often this occurs as the result of hæmorrhage in this region.

All the tracts which turn spinewards after leaving the nucleus lenticularis reach the tegment. Although not proved, it must be regarded as most probable that the nucleus lenticularis is connected with the crusta. Fibres coming out of the laminae medullares, as well as fibres from the nucleus itself, which enter the internal capsule, where they mingle with peduncular fibres, may perhaps be looked upon as establishing this connection.

With the exception of the fibres already described as passing through the nucleus lenticularis very little is yet settled as to the connections of the nucleus caudatus. We have some right to believe, however, that fibres pass from the nucleus caudatus directly to the crusta *via* the internal capsule, and by this route reach the region of the pons (forming part of the frontal pontine tract, p. 301).

The basal fore-brain bundle, which contributes a part of its fibres (as we know) to the formation of the ansa lenticularis, can be recognised throughout the whole series of vertebrates; more easily, indeed, in submammals than in mammals or in Man. None of the fibres of the stem-ganglion can be shown to extend farther caudalwards than the substantia nigra (*Edinger*).

Very extensive connections of the nuclei lenticularis et caudatus with the cortex cerebri are described by *Meynert*. He thinks that fibres from the frontal and parietal lobes reach the nucleus caudatus by way of the internal capsule. Such connections with the cortex have, however, been most emphatically set aside by *Wernicke* and other recent writers



on the subject, at any rate as far as concerns the outer segment of the nucleus lenticularis and the nucleus caudatus. The fibres seen by *Meynert* are regarded as at the utmost only fibres which are passing through the nucleus lenticularis, not ending in it. Only in animals can it be proved that the bundles of fibres in question by no means all pass through the nucleus lenticularis (*Kowalewski*). *Bianchi* and *Algeri* observed degeneration in bundles which stream into the nuclei lenticularis and caudatus, after extensive destruction of the motor regions of the cortex in dogs; *Ramón y Cajal* was able to see fibres which take rise from the pyramidal cells of the frontal lobe and traverse the nucleus caudatus, giving off collaterals to the nerve-cells contained in it as they pass through; and *Marinesco* succeeded by *Marchi's* method in demonstrating the presence of degenerated fibres in the stem-ganglia, especially the nucleus caudatus, after extirpation of the cerebellum. (The latter results were obtained from experiments on apes.) The existence of a tract between the cerebrum and nucleus caudatus must, therefore, be regarded as proved. Further, it is admissible to believe that the great grey masses of the putamen and nucleus caudatus are connected with other parts of the cortex cerebri by means of 'association fibres,' just in the same way as the several portions of the general cortex are united with one another.

*Sachs* sees this connection between the nucleus lenticularis and the cortex of the brain (frontal and parietal lobes and island of Reil) chiefly in a bundle which lies along the whole lateral border of the nucleus (fasciculus nuclei caudati, fasciculus subcallosus of *Muratoff*, association bundle of the nucleus caudatus). In frontal sections through the hemisphere it is seen in the lateral angle of the lateral ventricle, just under the corpus callosum. It runs from before backwards, constantly giving off fibres which enter the substance of the nucleus.

More detailed investigations into the **minute structure** of the ganglionic masses just described, to which in this connection may be added the nucleus subthalamicus and substantia nigra, are still desirable.

(a.) **Nucleus Caudatus.**—In that part of its head which lies upon the internal capsule, fibres that have streamed in from behind and below can be followed far towards its upper surface. Most of its nerve-cells are small, round, or fusiform. *Marchi* thinks that they belong to the type of sensory nerve-cells (?).

(b.) **Nucleus Lenticularis.**—Not only is the outer segment of this nucleus like the nucleus caudatus in colour, but it also agrees with it in minute structure. The bundles of nerve-fibres which collect towards the lamina medullaris externa have already found mention. The lighter colour of the globus pallidus depends upon a difference in quality in the ground-substance, although it would be difficult to define this difference histologically. It chiefly depends, however, upon the yellow pigment which its moderate-sized nerve-cells contain, as well as upon the number of medullated fibres which traverse the two inner segments of the nucleus lenticularis.



(c.) **Corpus subthalamicum**, mentioned first by *Luys* and described in greater detail by *Forel*. Its greatest thickness amounts to 3 to 4 mm., its breadth to 10 to 13 mm., its sagittal diameter to 7 to 8 mm. Its shape is that of a lens, lying on the pes pedunculi cerebri (fig. 151).

This body is characterised histologically by a close network of the very finest medullated fibres, amongst which coarse fibres are almost wholly wanting. Multipolar nerve-cells of moderate size containing light brown pigment are scattered about its substance. Only a few regions in the central nervous system are distinguished by so close a capillary network as the corpus subthalamicum; it possesses this latter character in most animals—the dog, amongst others.

(d.) **Substantia Nigra Soemmeringi**.—This substance contains spindle-shaped nerve-cells of moderate size, enclosing in Man little lumps of dark brown pigment. From one-third to one-half of the cell is usually filled up with this pigment, which does not appear until the completion of the third year. Between the fifth and sixth years the majority of the cells are pigmented, and the pigmentation appears to reach its maximum by the sixteenth or eighteenth year (*Pilez*). The cells of the locus cœruleus (p. 280) are distinguished from those of the substantia nigra by their round vesicular form and greater diameter. Pigment is never present in the cells of the substantia Soemmeringi in animals.

Many of the pigmented cells of the substantia nigra are distinctly pyramidal in shape. According to *Mingazzini*, the apical processes of these cells are directed upwards, the basal axis-cylinder processes downwards to the crusta, where they unite with the fibres of the peduncle; whence he infers that we may expect to find here conditions analogous with those in the cortex cerebri. The suggested arrangement of the nerve-cells is, however, hardly discoverable.

Of the functional meaning of the parts just discussed very little is known. A connection certainly exists between the nuclei caudatus and lenticularis, but so far we are unable to determine its nature. A detail that deserves attention is the very gradual fall of the high temperature which follows on injuries to the nucleus caudatus.

## 2. THE MEDULLARY CENTRES OF THE GREAT BRAIN.

The greatest extent of this mass of medullary substance, so considerable in size in Man, is seen in a section carried through the centrum semiovale Vieussenii on a level with the corpus callosum. It is made up of three systems of fibres:—

(1) Fibres which extend from the cortex cerebri to the ganglionic masses of the 'tween-brain, or deeper down to the mid-brain, hind-brain, after-brain, and spinal cord: the corona radiata Reilii.

(2) Fibres which connect identical areas in the two hemispheres: commissural fibres.



(3) Fibres, some shorter, some longer, which bring different spots in the cortex of the same hemisphere into functional association; collectively we shall term them 'association fibres' [fibræ propriæ].

So few medullated fibres are found in the human cerebrum at birth that it looks grey and gelatinous. Edinger's tegmental radiation alone appears in the eighth or ninth month of embryonic life. Between the second and third week after birth the pyramidal tract begins to myelinate. In sagittal sections it is easy to see how this tract extends from the internal capsule towards the two central convolutions, beneath which it forks, *ansa Rolandica* (*Parrot*). After the first month the occipital lobes begin to whiten, after the fifth month the frontal lobes; but the myelination of the fibres of the great brain is not completed until after the ninth month of extra-uterine life (*Parrot*).

The various parts of the cortex are supplied with fibres of the three kinds just named in very different ways and to a very different extent. *Flechsig* even goes so far as to think that the fibres of the corona radiata are confined to about one-third of the cortex, viz., the visual area in the fissura calcarina, the auditory area in the first gyrus temporalis, the olfactory area in the gyrus hippocampi, and the whole of the motor zone. Starting from the assumption that tracts which conduct centripetally (continuations of the posterior columns, etc.) enter the motor zone, he gives the name of 'sense-centres' to the region supplied by the fibres of the corona radiata, and terms the regions of the second class—those, that is, which enter into connection only with other cortical regions—'association-centres.'

But the connection between all parts of the cortex is not equally close, although we must assume that in the human brain these inter-cortical relations are rich and manifold in a degree corresponding to its high development. It is very difficult to bring incontestable proof that any two parts of the cortex are totally disconnected. In any case, an extremely intimate connection will be of service in promoting the highest possible degree of functional capacity. Thus, *Sachs* attempts to prove that the occipital lobe has hardly any intimate connections except with the temporal lobe, and only with the posterior part of that, and none whatever, perhaps, with the anterior part of the cerebrum. The temporal lobe, on the contrary, is connected with nearly all parts of the cortex of the brain.

(1.) **Corona radiata.**—The fibres of the corona radiata, considered as a whole, converge like an open fan towards the internal capsule—a crown of rays may be shown in dissected preparations, to rest upon the 'tween-brain. The region next above the internal capsule, where the fibres coming from various places meet the stalk of the fan, is termed the pedunculus coronæ radiatæ. It must be remembered, however, that some of the fibres of the corona radiata pass to the thalamus, and others to (or from) deeper-lying structures.

The following more important parts of the corona radiata may be distinguished:—

(a.) From the anterior part of the frontal lobe, the frontal pontine



tract and the anterior peduncle of the thalamus. Also fibres which take origin from the frontal and parietal lobes and are collected into a bundle which runs a sagittal course laterally to the nucleus caudatus (*Sachs*).

(*b.*) From the central convolutions and neighbouring areas, the pyramidal tract and perhaps also Edinger's tegmental system of fibres, as well as bundles for the thalamus.

(*c.*) From the posterior parts of the parietal lobe and also from the occipital lobe, fibres for the thalamus (running chiefly in its posterior peduncle), as well as fibres for the external geniculate and anterior quadrigeminal bodies, and also for the posterior part of the hinder segment of the internal capsule (sensory tracts of the sagittal medullary stratum).

(*d.*) From the temporal lobe, fibres for the thalamus, a part of which run in its inferior peduncle, while others join the sagittal medullary stratum. Of the last division the majority are probably not meant for the thalamus, but for the back of the internal capsule and so for the crusta. Fibres seem also to extend from the temporal lobe to the internal geniculate body. *Flechsig's* view that the fibres of the corona radiata are distributed over a third part of the brain-surface only is no longer tenable.

Beside these most important constituents of the corona radiata, it contains others, such as Edinger's basal bundle of the fore-brain (*ansa lenticularis*), and the olfactory bundle, as well as the fornix.

To what we have already said about the anatomical disposition of the **fornix** (p. 81), something must still be added here. The first point which we must bear in mind is that the fornix draws all, or nearly all its fibres through the fimbria from the cortex of the cornu Ammonis on the same side; but it may be considered certain that each pillar contains fibres from the cornu Ammonis of the opposite side.

The fornix contains many fibres which originate in the region of the cornu Ammonis and end in the corpus mammillare, being, therefore, analogous to the fibres of the corona radiata. A small portion of the fornix which streams on to the septum pellucidum [*præcommissural* fibres of Huxley] ought to be reckoned as fibres of association, since the septum pellucidum belongs to the cortex.

According to *Zuckerkindl*, these fibres belong to the olfactory bundle of the cornu Ammonis and pass into the central olfactory apparatus in front of the anterior commissure. At any rate, we may take for granted that the fornix is very intimately connected with the olfactory region. Other bundles from the columna fornicis also pass down in front of the anterior commissure, twist round it, and turn back immediately to reunite with the main stem. The *stria alba tuberis* (p. 430) should also be mentioned here.

Nor should we forget the fibres of the fornix which diverge from the columna fornicis, arch upwards, and pass backwards as the *striæ medullares thalami* (p. 419).

A part of the fibres of the pillars of the fornix crosses in the anterior decussation of the regio subthalamica shortly before reaching the corpora mammillaria.



Each **corpus mammillare** is divided into two separate ganglia—a mesial one containing small cells and a lateral one containing large nerve-cells. A large part of the columna fornicis (called its radix) pushes itself between the two ganglia, partly to enter their substance, partly to form their capsule.

Only a part of the fibres of the fornix ends in the corpus mammillare; the remainder run in very different directions, forming, for example, the bundles which cross behind it and on its dorsal side (inferior crossed root of the columna fornicis). Other less important connections of the fornix certainly exist (*vide Gudden, Honegger*).

Out of the posterior part of the mesial ganglion, which constitutes the bulk of the corpus mammillare, arises the bundle of Vicq d'Azyr (fasciculus thalamo-mammillaris, ascending crus of the fornix of Meynert) which first ascends directly and then bends more anteriorly to terminate in the tuberculum anterius of the thalamus. If, in the corpus mammillare, a simple turning over of the radix columnæ fornicis into the bundle of Vicq d'Azyr is not probable, an undeniable relationship between these two tracts nevertheless exists. A smaller bundle extending backwards to the tegment arises in the mesial ganglion (tegmental bundle of the corpus mammillare). It cannot be followed far, in Man especially, as its fibres very soon scatter.

The lateral ganglion also sends a bundle of fibres backwards to the tegment (pedunculus corporis mammillaris, Meynert's tegmental bundle of the corpus mammillare). In the rabbit it lies quite superficially on the inner border of the crusta; in Man it is situate more deeply. It is pierced by fibres of the oculomotor nerve, *Pcm* (fig. 149). Its subsequent fate in the region of the pons is not yet ascertained. It must be noted that each corpus mammillare passes over, on the anterior and external side, into a broad stem, the brachium corporis mammillare of Retzius.

Sometimes a bundle, about 1 mm. broad, is seen stretching, usually on the left side only, quite superficially, from the corpus mammillare over the tuber cinereum, and disappearing beneath the chiasma some 4 or 5 mm. from the mesial border of the crusta (*Lenhossék*). This bundle, stria alba tuberis, turns outwards beneath the tractus opticus, to the fornix of which it ought to be regarded as a detached fasciculus.

*Lenhossék* describes yet another bundle of fibres arising in the medullary covering of the corpus mammillare. It passes more deeply through the tuber cinereum in a sagittal direction forwards, and spreads out into the substantia perforata.

(2.) **Commissural Fibres of Cerebrum.**—By means of the corpus callosum, anterior commissure, and commissura hippocampi, a connection is effected between identical spots on the cortex of the two hemispheres; in Man, at any rate, it looks as if each individual area on the general surface of the great brain was without exception united to its corresponding contra-lateral area. It is not, however, certain that the commissural system for the several regions of the cortex is everywhere equally well developed. [*Sherrington* finds that secondary degenerations in the



corpus callosum do not extend from the injured area directly to the homologous spot on the opposite hemisphere, but show a tendency to spread out.]

(a.) **Corpus Callosum** (*Trabs*).—From that part of the corpus callosum which can be exhibited by simply drawing aside the two hemispheres and exposing the bottom of the great longitudinal fissure (free part of the corpus callosum), the fibres stream into the two hemispheres (radiation of the corpus callosum). In this free portion of the corpus callosum the fibres run horizontally, but soon after entering the hemispheres they diverge upwards and downwards to the parts of the cortex for which they are destined. Since the cerebral hemisphere exceeds the corpus callosum in length, it is clear that all the fibres of the latter cannot continue in the same frontal plane; but both at its front and back the fibres must form arches as they curve round to the front of the frontal and the back of the occipital lobe respectively. In front, at the genu corporis callosi, the fibres destined for the frontal lobes of the two hemispheres form the forceps anterior. In defibred preparations this shape is chiefly due to the deceptive appearance of fibres of the corona radiata, which come from the temporal lobe and seem to bend round into the corpus callosum. On this ground *Dèjerine* refuses to recognise the existence of a forceps anterior. The streaming out of the fibres of the rostrum corporis callosi into the convolutions of the two sides, may be termed, with *Henle*, the white commissure of the floor (commissura baseos alba).

The fibres of the corpus callosum destined for the occipital and temporal lobes pass through the splenium.

The occipital portion of the corpus callosum takes rise from the point at which the splenium bends round. It runs back as a strong column, concave medianwards (forceps posterior). The main body of these fibres passes, as the forceps major, to the cortex of the upper parietal lobule, in the upper part of the mesial wall of the posterior horn. They make a swelling on the mesial wall of the ventricle, known as the bulbus cornu posterioris. A little detached tract (forceps minor) courses in the lower wall of the posterior horn. The greater part of it goes to the gyri fusiformis et lingualis.

From the rolled-up posterior edge of the splenium the fibres of the corpus callosum pass off to the temporal lobe. They cling to the lateral wall of the lateral ventricle, especially in the inferior horn (tapetum). From this layer of fibres investing the outer wall of the inferior horn, fibres are constantly given off to the cortex of the temporal lobe.

In many cases in which the corpus callosum was absent, the tapetum has nevertheless been found well-developed (*Onufrowicz, Kaufmann*), whence the conclusion has been deduced that the latter received its fibres, not from the corpus callosum, but from the fasciculus longitudinalis superior (p. 434), or the fasciculus nuclei caudati (p. 425). But, on the other hand, cases have been described in which the tapetum was lacking, although the fasciculus longitudinalis superior was well preserved (*Mingazzini*). *Muratoff* found the tapetum intact after experimental destruction of the corpus



callosum, and is therefore inclined to admit no connection, or only the slightest, between the tapetum and corpus callosum; an opinion which is shared by *Déjerine*. On the other hand, again, *Anton* observed secondary degeneration of the contra-lateral tapetum as a result of softening of the splenium and forceps major; so that, although the question of the origin of the tapetum is not definitively settled, we have yet some justification for the view that a not inconsiderable portion of it belongs to the corpus callosum. The external capsule receives a considerable accession of fibres from the corpus callosum. On their way they have to cross fibres intended for the internal capsule (*cf.* fig. 20).

It may be regarded as certain that the corpus callosum provides for the whole of the surface of the cerebrum, with the exception of the inferior and anterior portions of the temporal lobes and the olfactory lobes (*tractus olfactorii*). *Beever* made the mistake of including the cuneus among the parts which receive no fibres from it.

The fibres of the corpus callosum used to be generally regarded as commissural fibres in the strict sense of the word, connecting only corresponding regions in the two hemispheres; but we are now certain that a great many of them (if not all) establish connections between parts of the cortex that are not equivalent. For instance, in the tapetum we find fibres which originate from the temporal lobe of one side, traverse the posterior part of the corpus callosum, and pass, through the forceps major of the other side, into the cuneus, thus constituting a crossed connection between the auditory and visual centres.

Since no single fibre can be isolated in its whole course from a certain spot on the cortex in one hemisphere to the corresponding spot on the opposite hemisphere, it will be readily apprehended that from time to time a voice is raised in favour of a different meaning for this part of the brain. *Hamilton*, in particular, erroneously asserts that the corpus callosum represents a great crossed communication between the cortex and the opposite internal and external capsules. On the other hand, the experiments of *Ferrier* and *Turner* seem to prove that numerous fibres from the thalamus opticus pass through the corpus callosum to the cortex of the contra-lateral hemisphere, so that crossed fibres would, as a matter of fact, course in it.

The upper surface of the corpus callosum is invested (as I shall explain when I come to describe the cortex of the gyrus fornicatus) with a thin layer of grey substance, which lies near the middle line and is divided into two longitudinal ridges, the *striae longitudinales medialis et lateralis seu nervi Lancisii*. In many brains they are but faintly marked.

In sagittal sections of the brains of many small mammals we find bundles of fibres which enter the corpus callosum from the medullary substance of the great brain immediately above and behind it (the gyrus fornicatus), run forwards more or less sagittally on its inner side, and finally enter the septum pellucidum (*fornix longus*).

In lower vertebrates and aplacental mammals there is no real corpus callosum present; in fact we invariably find that the more highly the brain



is organised the stronger is the development of the corpus callosum. In the brains of low vertebrates the commissura hippocampi is almost the only thing that represents it. Complete or partial deficiency or abnormal shortness of the corpus callosum has been repeatedly observed in Man.<sup>1</sup>

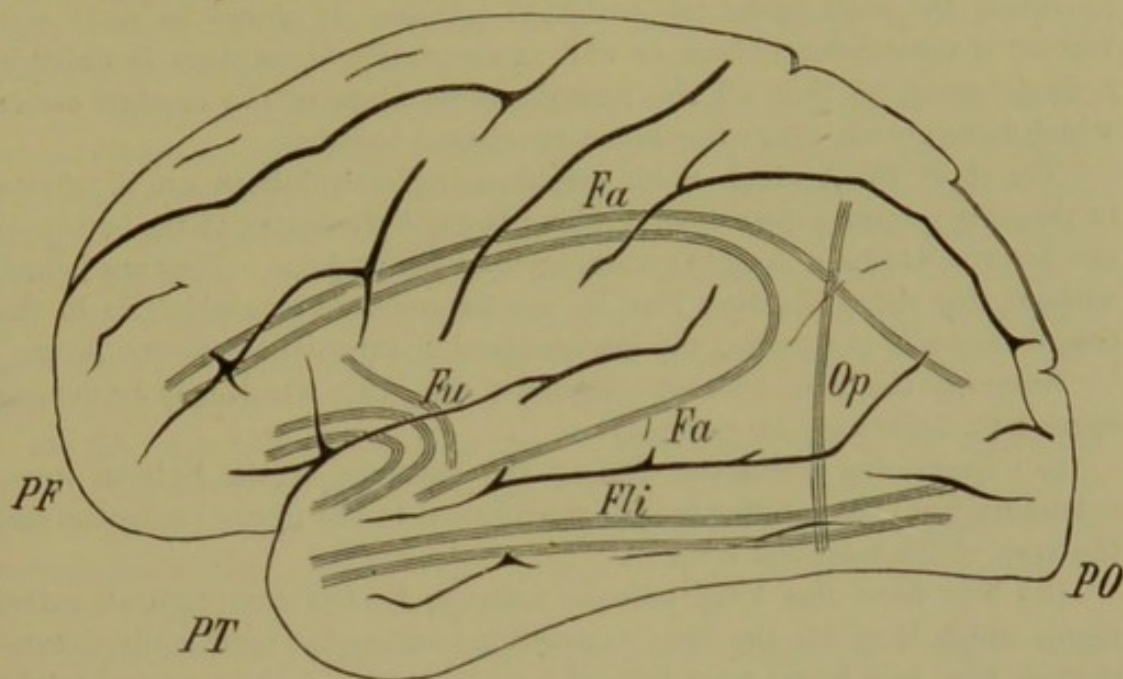


Fig. 192.—Diagram of the long associating tracts of the cortex cerebri.—PF, Frontal pole; PT, temporal pole; PO, occipital pole; Fa, fasciculus arcuatus; Fu, fasciculus uncinatus; Fli, fasciculus longitudinalis inferior; Op, fasciculus occipitalis perpendicularis.

(b.) The **anterior commissure**, which is an accessory to the corpus callosum for the connection of the cortex of the olfactory lobes and parts of the temporal lobes, has already been described in detail (*cf.* p. 331). In cases of deficiency of the corpus callosum the anterior commissure is sometimes more or less completely absent.

(c.) The **commissura hippocampi** (commissure of the fornix or of the cornu Ammonis) consists of the transverse fibres of the psalterium which connect the two cornua Ammonis. By many it is looked upon as a rudimentary corpus callosum. We find it in monotremes, birds, amphibia, and reptiles, in all animals, that is to say, in which any structure analogous with the cornu Ammonis is present. In all these classes the corpus callosum is almost or entirely wanting.

(3.) **Fibres connecting together Different Areas on the same Hemisphere.**—It is necessary to distinguish between short fibres which connect together neighbouring cortical regions and long or considerable

<sup>1</sup> [The anterior and hippocampal commissures are alone present in Monotremes and Marsupials. Their cortex is chiefly represented in the temporal lobe and hippocampus of higher mammals. The development of the corpus callosum is proportional to that of the remaining cortical fields. It is not improbable that fibres are transferred from one or both of the primitive commissures to the corpus callosum; but, on the other hand, it is possible that the absence of the latter in proto- and metatheria indicates that the whole of their cerebral cortex is homologous with the temporal lobe and hippocampus of higher mammals.]



tracts which unite together parts of the cortex situate some distance away from one another. Collectively the two sets of fibres are spoken of as belonging to association-systems, since they are regarded as systems for bringing into functional connection distant parts of the brain and so providing the mechanism for concerted actions. It would be more convenient if commissural fibres, as well as association-fibres, were included in a single group, so that all the homodesmotic fibres of the cerebral cortex which have an analogous function were classed together.

The short fibres which unite neighbouring convolutions are to be seen in properly prepared dissections, arching beneath the cortex at the bottom of the fissures, U-fibres, Arnold's fibræ arcuatae seu propriæ. They are joined, without any sharp dividing line, by similar arcuate fibres which lie in the deeper layers of the cortex, the intra-cortical or external association-layer.

Amongst the long association-bundles (fig. 192) which may be demonstrated by defibreing are reckoned :—

(a.) Fasciculus uncinatus, *Fu*, at the entrance of the Sylvian fossa, extending from the inferior frontal convolution to the gyrus uncinatus and the apex of the temporal lobe.

(b.) The fasciculus longitudinalis inferior, *Fli* (stratum sagittale externum), which is of all the long association-bundles the most easily demonstrated, runs as a broad tract from the anterior part of the temporal to the apex of the occipital lobe. It is also said to give off fibres to the external capsule. It surrounds the optic radiations of the occipital lobe like the half of a saucer.

(c.) The fasciculus arcuatus, *Fa* (seu longitudinalis superior, upper longitudinal bundle), consists of sagittally-disposed fibres, beneath the inferior and middle frontal convolutions, running partly towards the occipital lobe and partly arching round towards the apex of the temporal lobe; it is not easy, however, to make a good preparation of this tract, as it is closely interwoven with the fibres of the corpus callosum. Degeneration can never be followed far in this bundle; it probably consists entirely of short fibres connecting convolutions not very far apart.

(d.) The cingulum is an arched tract which lies in the medullary substance of the convolution of the same name, and so describes a great arch between the substantia perforata anterior near the mesial surface of the brain and the apex of the parietal lobe. For the greater part of its course the cingulum lies up against the corpus callosum along the line of junction of its body and its radiating fibres. In frontal sections of the brains of animals it can, as a rule, be recognised by its circular cross-section.

The separate fibres of the cingulum do not appear to run its whole length, or, indeed, any great part of it. It is probably composed of fibres which only keep this course for a short distance. Those contained in the part above the corpus callosum turn aside in front into the centrum semi-ovale, while behind they probably have their roots in various parts of the cortex (*Beevor*). Accordingly, it is by no means impossible that fibres from the corona radiata course in the cingulum.



(e.) The perpendicular occipital fasciculus of Wernicke, *Op* (cf. fig. 19, *Fov*), descends from the upper angle of the inferior parietal lobule vertically to the lobulus fusiformis.

(f.) By the name of fasciculus lobuli lingualis, *Vialet* describes a bundle which courses from the under side of the calcarine fissure to the convex surface of the occipital cortex.

(g.) The fasciculus occipito-frontalis, situate in the lateral angle of the lateral ventricle, may partly correspond to the fasciculus nuclei caudati, fasciculus subcallosus (p. 426). Here also lie the bundles of fibres of the corona radiata described by *Sachs* as coming from the frontal and parietal lobes. *Déjerine's* view is that this bundle originates mainly in the gyri frontales, courses back above the nucleus caudatus and beneath the corpus callosum, and streams into the cortex of the occipital and temporal lobes; forming the tapetum on its way (cf. p. 431).

On the outer side of the cingulum we come upon the place where the fibres of the corpus callosum and the internal capsule meet one another at right angles and interlace. It is immensely difficult in this region to distinguish individual tracts of fibres; farther outwards these two sets of fibres are more in accord as to their course.

The fibres of the external capsule have a fan-shaped, downwardly-converging course, corresponding to the disposition of the convolutions of the island of Reil. They seem to belong exclusively to the cortex of the island and to have nothing to do with the lateral segment of the nucleus lenticularis. Some of the fibres extend, as already mentioned, towards the corpus callosum.

It is obvious that all the fibre-tracts which establish connections between the several parts of the cortex (in which category I include the commissural fibres) must be of the highest functional importance, since in them we must seek for the most important mediators in associating presentations of sense. We find, accordingly, that in the more highly organised brains the commissural and association systems are peculiarly well developed; and we may fairly draw a parallel between their higher development and the capacity for more varied and complicated intellectual activity.

### 3. CORTEX CEREBRI.

The wall of the anterior cerebral vesicles, both primary and secondary, but especially the latter, develops into the grey substance of the cortex cerebri. Certain parts of the developed wall of the anterior cerebral vesicle do not seem to enter into the formation of the superficial layer of the great brain; nor do they either in date of development or in histological characters agree with the cortex cerebri in the stricter sense of the term. Further embryological observations are necessary to justify the conception that they really are homologous with the cortex. We have already made the acquaintance of some of these portions of the brain which



do not look at the first glance as if they ought to be accredited to the cortex—viz., the grey substance of the tractus olfactorius, the nucleus caudatus, and the putamen.

If we cut, no matter where, at right angles into the surface of the hemisphere, the cortex (in the limited sense of the word) appears as a dark bordering band. The breadth of this band not only varies in different individuals, but in the same brain it depends upon the locality. It varies from 1.5 mm. to 4 mm., and is invariably thicker at the apex of the convolutions than it is in the fissures. Its maximum breadth is attained at the upper part of the central convolutions and in the lobus paracentralis, its minimum near the occipital pole. In old age, with advancing atrophy of the brain, the diminishing thickness of the cortex is very noticeable.

Even in microscopical observation of fresh brains a stratification of the cortex parallel to the surface is evident, owing to the different colour of its layers. The differences in colour of the several layers are not equally distinct in all brains or in all parts of the cortex of the same brain.

*Kölliker* distinguished an outer white, middle grey, and inner yellowish-red layer. The narrowest of the three is the white layer on the surface, the other two are about equally broad. Between the two inner layers lies a not well-defined white band, while another band, or even two bands, sometimes occupy the middle of the inner layer; these are known as *Baillarger's stripes* (outer and inner). Hence the reader will gather that *Baillarger* distinguished six layers in the cortex.

This stratification is most likely to be seen in the superior frontal or anterior central convolutions. In the neighbourhood of the calcarine fissure, extending a little into the surrounding convolutions, especially the cuneus, *Baillarger's* outer stripe although narrow is sharply marked and easily seen in all brains (fig. 27). It has received the name in this locality of *Vicq d'Azyr's stripe* owing to its description for the first time by this anatomist. Before him, however (on February 2, 1776), *Gennari* saw this band traversing the cortex, 'lineola albidior admodum eleganter,' and described it very exactly, considering the topographical knowledge of the time. He figured it as well as the other stripes of *Baillarger*. It would, therefore, be only just to re-christen *Vicq d'Azyr's stripe* at any rate as *Gennari's stripe* (lineola albida *Gennari*). This name, however, is given by some to *Baillarger's stripe*.

Just as with the naked eye the appearance of the cortex is not the same in all regions, so we find that (unlike the cortex cerebelli) its microscopic structure varies in its several parts. An exact account of all the local differences in minute structure in the cortex cerebri is not yet available, although the more important details with regard to certain regions have been described.

We will commence our description with a section taken from the posterior end of the middle frontal convolution, and subsequently point out the more important features by which other regions are distinguished. The stratification visible with the naked eye in the cortex of a fresh brain is produced by the arrangement of the various tissue-elements



of which it is composed, not, it is true, in definite strata, but still in layers with a certain amount of regularity.

The layers of the cortex cerebri are usually classified according to the form, size, and distribution of their nerve-cells. We shall, there-

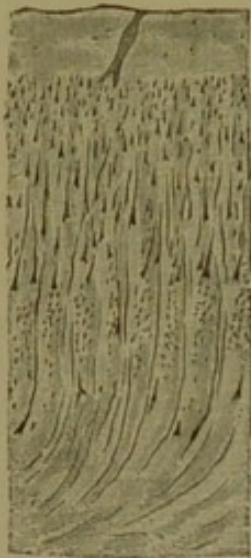


Fig. 193.

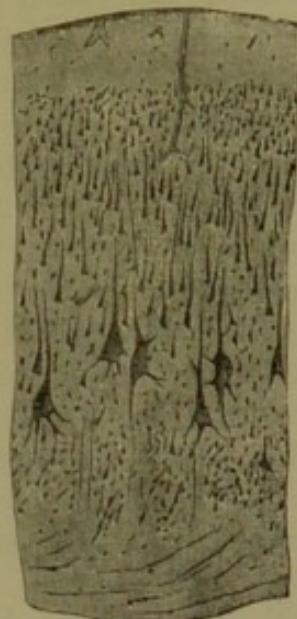


Fig. 194.

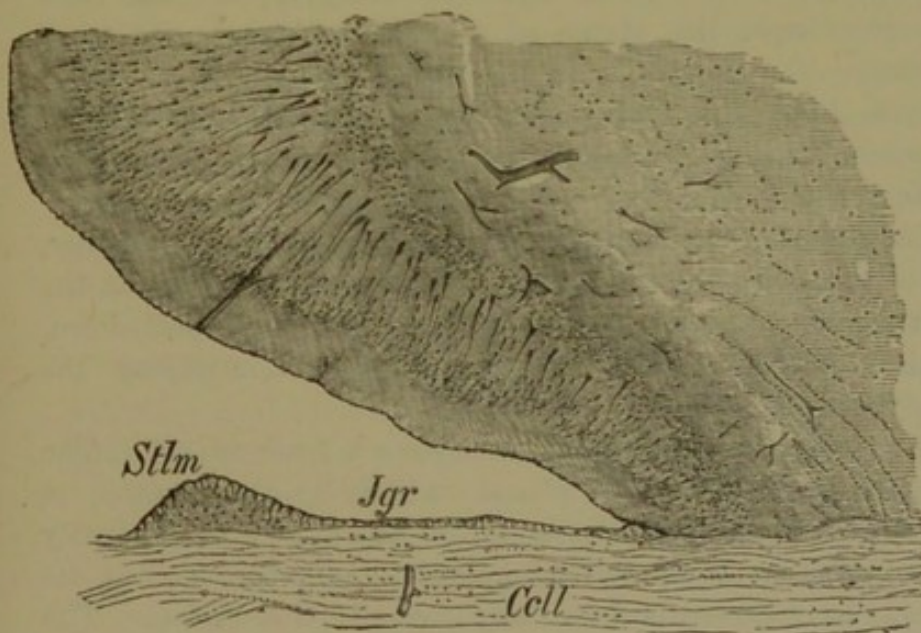


Fig. 195.

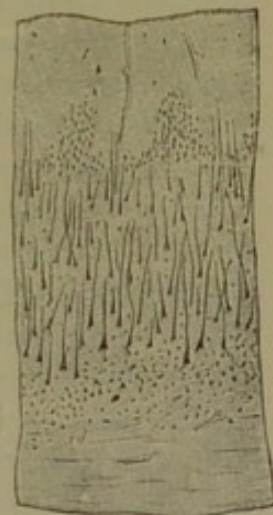


Fig. 196.

Fig. 193.—Vertical section through the human cortex cerebri where it covers the posterior part of the middle frontal convolution. *Carminé staining. Magn. 20.*

Fig. 194.—Cortex of the lobulus paracentralis.

Fig. 195.—Cortex of the gyrus cinguli. —*Cell*, corpus callosum; *Jgr*, indusium griseum; *Stlm*, stria longitudinalis medialis.

Fig. 196.—Cortex of the subiculum cornu Ammonis at its most projecting part.

fore, study first a carmine-coloured preparation; since in silver preparations we run the risk of seeing only a limited number of cells, and those not equally in all layers. The direction in which the section is cut should be such that the nerve-fibres which stream into the cortex are divided,



as far as possible, in the direction of their course. This direction can be determined by breaking a small piece of hardened brain, including a portion of medullary substance. The plane of cleavage corresponds to the direction of the bundles of fibres, as can be seen by the characteristic radial striation. To obtain good preparations of the cells of the cortex, it is advisable merely to harden the piece of tissue in chrome-salts, and to cut it under water with Gudden's microtome, avoiding the use of alcohol and celloidin.

Immediately beneath the pia mater which limits it towards the epicerebral space, a layer 0.25 mm. thick is met with (layer poor in cells, layer of scattered cortical bodies, neuroglial layer, stratum moleculare, ependyma-formation), in which small nerve-cells are scattered about irregularly in an apparently homogeneous ground-substance (fig. 193). On its outer border is to be seen a narrow stratum (10 to 30  $\mu$  in thickness) consisting exclusively of a close gleial feltwork containing many spider cells. It gives to the preparation when slightly magnified a dark contour.

The second layer (of small pyramidal cells, outer nerve-cell layer) is about as thick as the molecular layer from which it is sharply marked off. It contains a great number of nerve-cells, not more than 10  $\mu$  in height, closely packed together. They are for the most part pyramidal in shape, the apices of the pyramids being directed towards the surface.

The third layer, 1 mm. thick (layer of large pyramids, formation of the cornu Ammonis, middle nerve-cell layer), is not well marked off from the preceding one.

The pyramidal cells become more widely separated from one another, and larger in size the farther we descend from the surface, so that the largest (as much as 40  $\mu$  in breadth) are to be looked for deepest down. These large cells afford us the best opportunity of studying the peculiarities of pyramidal cells.

The pyramid may be imagined as evolved from a fusiform cell. The spindle-cell must be supposed to be placed radially to the surface; it gives off two chief processes, the outer one of which is very gradually derived from the cell-body, being formed indeed by a tapering-off of its substance; it can be followed a long way towards the surface. The other process originates more suddenly from the cell with which it is connected by a conical base; it turns more or less directly towards the medullary substance. Besides these two chief processes the cell gives off a number of secondary processes (from 4 to 12) with very wide bases. The largest and most regularly disposed of these come off from the deepest part of the cell-body, which gains, therefore, a considerable girth. The cell acquires in this way the shape of a cone or pyramid with its point directed outwards.

The processes are named in terms applicable to this pyramidal shape. The first of the chief processes which runs towards the periphery is named the apical process, the other one, which passes deeply, the basal process.



The accessory processes which come off from the circumference of the base are named lateral basal processes; all the rest are simply lateral processes.

The apical process can be followed, sometimes as far as the layer of small pyramids, but hardly ever into the molecular layer in carmine-stained preparations. On its way from the cell it gives off a variable number of fine side branches, which have somewhat thickened bases and lie at right angles to the apical process, dissolving farther on into the finest possible network. The chief process thus becomes gradually thinner and more delicate.

The middle basal process (fig. 198, *a*), which is often very difficult to find, is supposed to be continued directly into a medullated fibre, and hence is termed the axis-cylinder process. The axis-cylinder process, in exceptional cases, comes off from the side of the cell. Even under the most favourable conditions it is only rarely possible to prove that it passes directly into a medullated fibre.

The accessory processes are distinguished from the chief processes by the manner of their division, which is dichotomous; only after continued forking do they end in the network.

The protoplasm of the pyramidal cells is finely granular; sometimes (it must be remembered that all this refers to carmine preparations) a delicate striation can be recognised. After the twentieth year of age, a little clump of light-yellow pigment is always found in the cell, usually nearer to its base than apex. The nucleus is round or oval, or imitates on a diminished scale the pyramidal form of the cell. Cells with round and cells with pyramidal nuclei occur side by side. It is not yet ascertained whether this difference in the form of the nucleus is associated with a difference of function or is only a result of hardening.

The nucleolus is conspicuous owing to its high refraction.

Owing to the manner in which the apical process arises it is impossible to determine the length of the cell, the division between its body and the apical process being an arbitrary one.

The nerve-cells of the cortex cerebri, especially the pyramidal cells, are, on various grounds, considered as concerned in carrying out psychical functions; although it is not permissible to place the 'seat of perception' in them without further ado. It is very probable that the largest pyramids have a psychomotor rôle.

A pericellular space of varying breadth surrounds the larger pyramidal cells. It often contains from one to five cells, presumably lymphoid [leucocytes].

The nerve-fibres come up from the medullary centre in close bundles easily seen in carmine preparations; they pass radially outwards towards the surface in regular order to lose themselves one after another in the neighbourhood of the third layer. The spaces between the groups of nerve-fibres are occupied by nerve-cells arranged in radial columns.

Not a few gleia-cells (spider cells) with many processes are found



throughout the whole thickness of cortex; they are seen most distinctly in the zone of the large pyramids.

The fourth layer of the cortex (layer of small irregular nerve-cells, granule formation, mixed nerve-cell layer) is about 0.3 mm. wide in the section under description, and fairly easy to distinguish from the third. The spaces between the radiating bundles, which now contain more fibres, are occupied by small cells still arranged in columns. These cells are about 8 to 12  $\mu$  in diameter, round, angular, or irregular in shape, and almost all indubitably nervous. Very little can be alleged with certainty as to the number and further course of their processes by this staining method. It may be noticed that similar irregular, polymorphous cells are to be found scattered irregularly through all the layers of the cortex; and not a few large pyramids, and small pyramids, too, are met with amongst the small polygonal cells.

In the fifth and deepest layer the bundles of medullated fibres coming from the centre claim the largest share of space. The small irregular cells become rapidly sparser, but the fourth layer is not marked off sharply from the fifth. In the fifth layer cells of moderate size make their appearance, presenting every gradation of form from spindles to pyramids (layer of fusiform cells, claustral formation). Since, for the most part, they correspond in direction with the medullated fibres, a single process, similar to the apical process of the pyramid cells, is seen, as a rule, especially at the apex of the convolution; at the bottom of the fissures, however, it often happens that these cells are disposed parallel with the surface, in a manner corresponding to the course of the associating arcuate bundles. In this situation the layer is narrow and sharply marked off from the medullary substance; whereas at the apex of the convolutions the cells spread into the medullary substance, from which the cortex is not, therefore, clearly limited.

In our description of the cortex cerebri we have followed *Meynert*, in recognising five layers as the typical arrangement. Certain of the layers may again be divided, as we have seen. The fourth and fifth layers are not always clearly distinguishable, and, consequently, many anatomists rank them as one (the layer of small nerve-cells, or inner nerve-cell layer).

The fibres vary very greatly in different individuals, both as to number and calibre, and the carmine method teaches us little with regard to their behaviour. Exner's perosmic acid method or Weigert's method must be used for this purpose, or, better still, Wolter's modification. Pal's method of medullary-sheath staining is often unsatisfactory for cortex.

*Greppin* proposes cutting the brain (either fresh or after from four to twelve weeks' hardening in Müller's fluid) with the freezing microtome; the sections to be put for ten or fifteen hours in a burgundy-red watery solution of safranin, washed in water, spread out on a slide, dried with blotting-paper, and examined in a drop of 33 per cent. solution of caustic potash. The violet or dark-red nerve-fibres can then be clearly seen.



These preparations will not keep for more than half an hour at longest.

The great wealth of medullated fibres which *Exner* was the first to exhibit to perfection, can only be seen in pieces of cortex which have been placed in the hardening fluid a few hours after death.

In such preparations we see just beneath the pia mater, a border of gleia, *a* (fig. 197), destitute of nervous elements. Beneath this, corresponding to the outer half of the stratum moleculare (*1*) follows a layer (*b*) almost entirely occupied by medullated fibres. Most of these fibres are thin, but some coarse ones occur amongst them, especially in the gyrus centralis anterior; they run parallel with the surface, tangential to the arc which the convolution forms (tangential border zone, zonal fibres, *Exner's* plexus, plexus externus, covering layer). The zonal layer is less rich in fibres in the frontal lobe than in many other parts of the brain. In the inner part (*c*) of the molecular layer is found a moderately close network of fine medullated fibres crossing one another at various angles, but running parallel, in the main, with the tangential fibres.

A similar network (*d*) occupies the layer of small pyramids (*2*).

In the layer of large pyramidal cells (*3*) the fibres are arranged radially; they are collected into bundles which are more definite in its deeper parts. Single fibres from this layer can be followed into the border zone. In the middle of this layer a region (*f*) is found, which appears in preparations made according to *Weigert's* method as a dark band, the number of interlacing fibres being very great, and the feltwork close. This layer corresponds to the outer stripe of *Baillarger* (plexus internus, intermediate layer, or *Gennari's* stripe).

In the area marked *g*, which corresponds partly to the fourth and partly to the fifth layer of the cortex, the radial fibres are not only close-set and conspicuous, but the bundles contain more thick fibres than they do further outwards.

In the middle of the fourth layer the network of fibres again becomes closer, making a second dark band, *h*, which corresponds to *Baillarger's* inner stripe (external or intra-cortical association-layer); it is narrower and less marked than the band *f*.

We have already seen in carmine preparations that the fibres which radiate outwards from the medullary centre occupy the greater part of layer *5*.

The layer marked *i*, therefore, corresponds to the deepest part of the fourth, and the whole of the fifth layer.

*Edinger* gives the name of 'inter-radial nerve-web' ('Flechtwerk') to the feltwork of fibres below *Baillarger's* outer stripe, on account of the numerous radial bundles which traverse it. He proposes the term 'super-radial nerve-web' as a suitable designation for the upper layers.

*Schwalbe* agrees, on the whole, with *Edinger* in recognising two chief zones, of which the inner comprises the bundles of radiating fibres, while in the outer, which is of about the same thickness, the bundles quickly fall to pieces. *Baillarger's* outer stripe, *f* (fig. 197), about forms the boundary



between the two, which lies, therefore, in the middle of the third layer, not, as often stated, in the line between the second and third layers.

The method of impregnating with silver or sublimate gives us a much clearer insight into many points connected with the structure of the cortex of the great brain.

We will now begin by examining the different elements of the cortex cerebri as exhibited by means of impregnation with metals, and proceed, by combining them, to give a picture of the organ.

**I. Nerve-Cells.** (a.) **Pyramidal Cells** (figs. 198 and 199, 1, 2, 3).—These are characteristic of the cortex of the great brain, and far outnumber the other nerve-cells found there; we will therefore give them the first place.

In the majority of pyramids the axis-cylinder process (figs. 198, *a*, 199, *x*) is easy to recognise. It almost always starts from the base of the pyramid, often from a lateral basal protoplasmic process, and courses, as a fine black thread, fairly straight downwards into the medullary substance. If the pyramidal cell lies at the apex of a convolution, the axis-cylinder process continues in its original direction; but if at the side, it bends round at nearly a right angle in the medullary substance. It gives off a number of collaterals at right angles, especially in the first part of its course. These run horizontally for awhile, and soon break up into terminal ramifications. The axis-cylinder process frequently divides in the medullary substance into two branches, which are said to continue their course in opposite directions.

The behaviour of the dendrites is variable, as has already been observed. Those which start from the base of the pyramid (lateral basal processes), or from the side of the cell-body, run, for the most part, horizontally, forking repeatedly as they

proceed. Their terminal branches sometimes extend a long way. *Kölliker* draws attention to the fact that some of these basal processes,

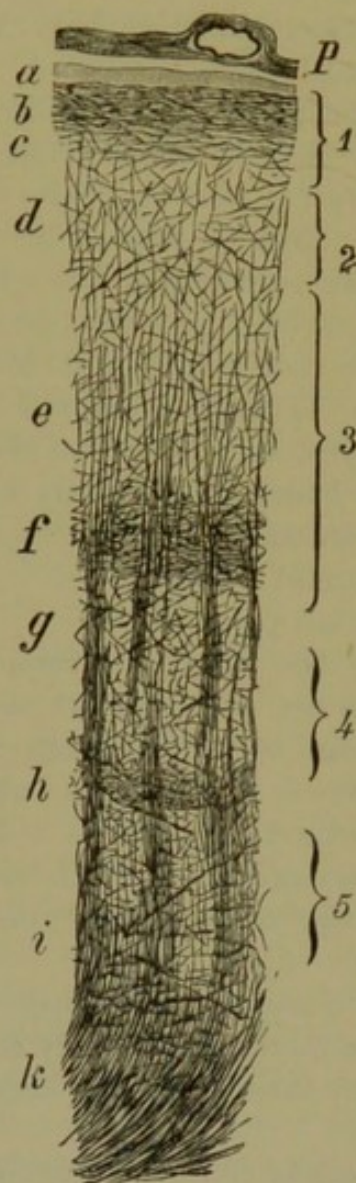


Fig. 197.—Cortex cerebri (frontal lobe). *Weigert's colouring. Magn. 50.*—*P*, Pia mater; 1–5, Meynert's five layers; *a*, layer of superficial gleia; *b*, layer of tangential medullated fibres; *c*, deeper part of the molecular layer; *d*, network of fibres in the layer of small pyramids; *e*, outer part of the third layer; *f*, external stripe of Baillarger; *g*, fibre-network of the third and fourth layers; *h*, internal stripe of Baillarger; *i*, deepest part of the fourth and fifth layers; *k*, medullary centre.



notably those which course obliquely, are remarkable for their great length.

The apical process (fig. 198, *s*), which originates by the gradual attenuation of the cell-body and courses perpendicularly to the surface, gives off, on the contrary, only fine side-branches at first, at right angles to its course, and does not divide until it reaches the border between the layer of small cells and the molecular layer. In the latter it usually divides several times, all the branches, however, retaining, on the whole, the perpendicular direction. Not till they reach the outermost parts of

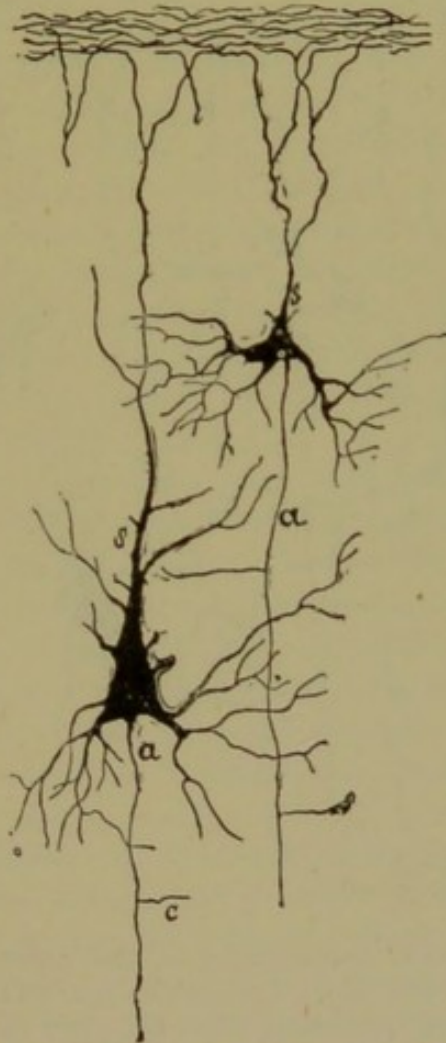


Fig. 198.—Two pyramidal cells from the cortex cerebri of a new-born puppy. *Silver colouring*.—*a*, Axis-cylinder process; *c*, collateral; *s*, apical process. The other protoplasm processes are not lettered.

the molecular layer do they bend round and take a tangential course, parallel to the surface. It is hardly possible to tell, with certainty, where they end.

In many preparations the molecular layer presents an almost impenetrable striation from the enormous number of apical processes which divide in it.

In embryos and quite young animals especially, the dendrites of the pyramidal cells look as if thickly set with fine prickles or granules. This hoarfrost-like investment helps us to distinguish the dendrites from the



axis-cylinder process, but it is still very doubtful whether it really belongs to the tissue of the process, or merely settles upon it from without.

[These 'thorns' are not limited to young animals. They occur at all ages. The fact that they are most conspicuous in young cells in which the soft neuroplasm which attracts the silver salt is relatively more abundant than in old cells is a confirmation of the *translator's* theory, that thorns are the portions of the non-staining, conducting fibrils along

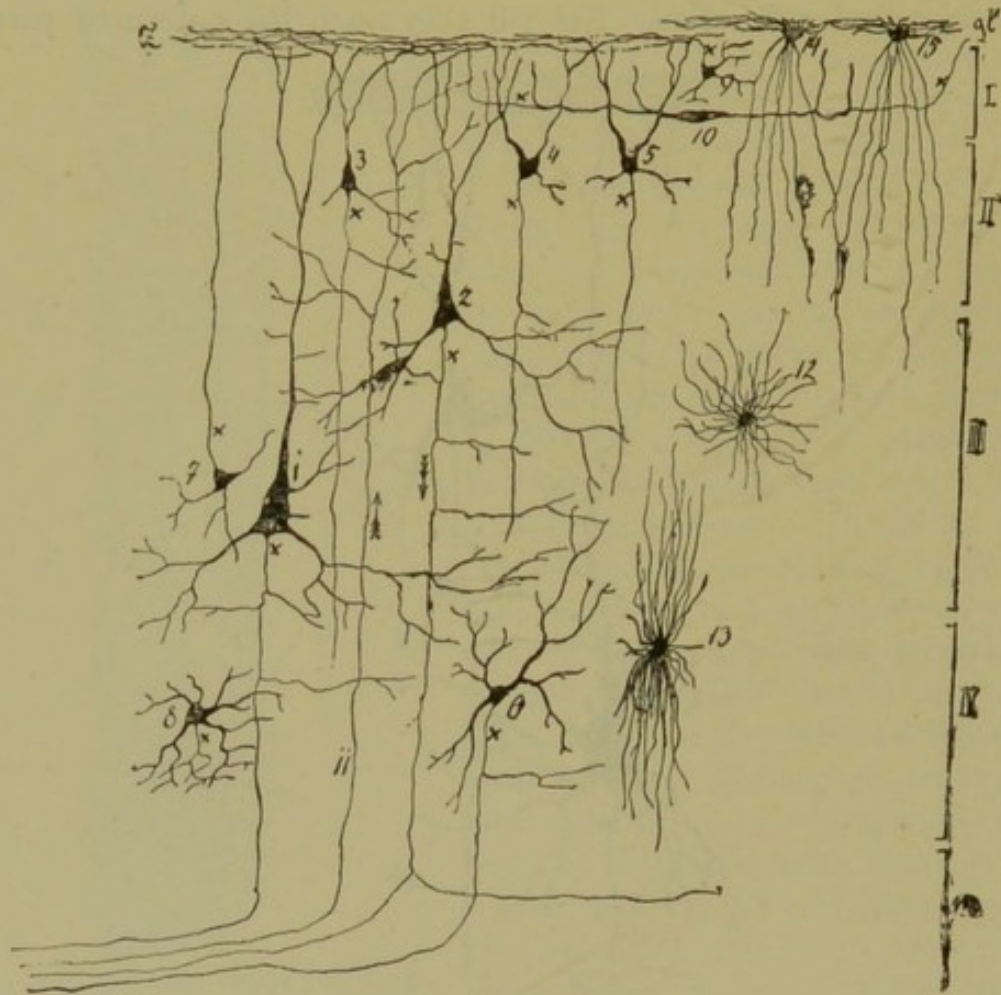


Fig. 199.—Semidiagrammatic representation of the cortex cerebri after impregnation with silver.—*gl*, Glia-layer; I, molecular layer; II, layer of small pyramidal cells; III, layer of large pyramidal cells; IV, layer of polymorphous nerve-cells (fourth and fifth layers of *Meynert*); *m*, medullary layer; 1, 2, 3, various pyramidal cells; 4, 5, uppermost cells of the small-celled layer; 6, polymorphous cell; 7, a Martinotti's cell; 8, a Golgi's cell; 9, small nerve-cell from the molecular layer; 10, a Cajal's cell; 11, ascending nerve-fibre from the medulla; 12, 13, glia-cells of the cortex; 14, 15, glia-cells of the glia-layer. The axis-cylinder processes of nerve-cells are marked with a cross, X.

which an outflow of cell-plasm has occurred (*vide ante*, p. 155). The great success of the chrome-silver method when applied to embryonic or young tissues confirms the view that the reaction affects some constituents of the cell-plasm and not the conducting fibrils.]

The above description applies to most pyramidal cells, but in the case of many of the small pyramidal cells in the outer part of the second layer



(4, 5) we meet with an apparent exception. In these the division of the apical process takes place close to the cell, sometimes at the very outset, and the shape thus produced may bear but little resemblance to a pyramid. We shall find others (fig. 197, 4, 5) in which the apex of the cell-body itself is cleft, and two separate apical processes course toward the surface (*cellulæ bicornes*).

The axis-cylinder processes of the largest pyramidal cells are often conspicuously thicker than the rest.

(b.) **Other kinds of Nerve-Cells in the Cortex Cerebri.**—In all except the topmost layers we find, besides single pyramidal cells, round, triangular, or fusiform nerve-cells, known as polymorphous cells (6). These also send their axis-cylinder processes down to the medullary layer, while the dendrites turn, for the most part, outwards, dividing frequently as they proceed, but never reaching the molecular layer. Single dendrites occasionally course down to the medullary layer.

*Martinotti* has described triangular or spindle-shaped cells (7) which occur sometimes among the pyramids, but more usually in the deeper layers. The axis-cylinder processes of these cells course outwards, and bend round in a horizontal direction in the outermost parts of the molecular layer.

Cells of Golgi's second type, or Golgi's cells (p. 149, fig. 59), are also found in the brain cortex (8).

In the molecular layer, too, we meet with isolated nerve-cells, usually small and irregular, with the axis-cylinder process directed towards the surface, where it probably takes a horizontal course (fig. 199, 9). These known as Cajal's cells (10) have aroused a special interest. They usually lie in the deeper parts of the molecular layer, and exhibit marked peculiarities. The cell-body is triangular or spindle-shaped; a protoplasmic process goes off from either side, and runs for some distance. It sends a number of little lateral branches to the periphery, and finally bends round in the same direction.

In most cases a delicate fibre takes rise from the point where the protoplasmic processes bend round, and proceeds in the same direction, also giving off collateral branches towards the surface. This is supposed to be the axis-cylinder process. Since other supernumerary axis-cylinder processes sometimes start from the protoplasmic processes; these Cajal's cells seem to possess as many as three or four.

These peculiar and (as it seems) imperfectly-understood cells have hitherto only been found in the brains of young animals and of embryos (human as well as animal). Their presence in the brain-cortex of adults must therefore be regarded as very questionable, although some of the cells of the molecular layer are certainly nervous in character.

**2. Nerve-Fibres.** (a.) **Radial fibres.**—These are either axis-cylinder processes of the pyramidal and polymorphous cells, and consequently conduct corticofugally, or they represent fibres which ascend from the medullary layer, give off a number of collaterals in their passage through the cortex, and, for the most part, extend to and break up in the molecular layer (fig. 199, 11). These latter are corticopetal fibres.



With regard to the first kind, there is nothing to add to what has already been said; the second kind take rise from remote cells to which it is impossible to trace them back. They may come from the cells of the cortex on the same side, or (through the corpus callosum) from those of the opposite side, or from the cells of deeper-lying grey masses.

(b.) **Tangential and Oblique Fibres.**—These are densest in the zonal layer, Baillarger's stripe, and the external association-layer.

The zonal layer merits special attention. Here we find nervous fibres which must be looked on partly as medullated, partly as non-medullated fibres, and, finally, as the outspread branches of dendrites. The medullated fibres either originate from the axis-cylinder processes of Martinotti's cells (7), or belong to fibres which ascend from the medullary substance (11) and end here. The cells of the molecular layer may also be of some importance in this connection. The terminal branches of all these fibres are destitute of myelin. A very great number of the interwoven fibres of the zonal layer are, however, the dendrites of pyramidal cells, which here bend round horizontally.

Baillarger's stripe is largely composed of collaterals of the axis-cylinder processes of pyramidal cells.

The medullated fibres of the external association-layer can with difficulty be traced back to their source. It is likely that we have here to do with association-fibres, many of which either start from or enter into connection with the polymorphous cells of the deepest layer.

(c.) **Gleia-Cells.**—These (12) are found in great numbers in all parts of the cortex, and give off processes in every direction. Sometimes, especially in the deeper layers, we meet with cells of this class which send two particularly rich tufts in opposite directions, to the centre and to the periphery (13).

On the very surface of the brain-cortex, above the zonal layer, is a stratum of peculiar gleia-cells, from which thick tufts of gleia-fibres pass perpendicularly down into the molecular layer (14, 15), while other fibres go off horizontally, and form a superficial plexus of gleia.

A superficial cortical layer of closely interwoven gleia-fibres, varying in breadth from 3 to 30  $\mu$ , can be specially well exhibited in the cortex of the great brain. It becomes broader in advanced age, and the individual fibres grow coarser. Their course in the cortical layer is variable, but, on the whole, obliquely tangential. From this layer masses of fibres stream inwards, usually taking an obliquely radial course, and can often be followed to the lower border of the layer of small cells. In the deeper layers of the cortex *Weigert* found neurogleia only in single fibrils, often separated by wide intervals. In the medullary substance, on the contrary, a rich network of neurogleia is again present.

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Although the investigation of the structure of the cortex of the great brain is by no means complete, and although, in particular, many of the facts already known cannot be demonstrated in the case of adult Man, we



are nevertheless in a position to form an opinion on the main points, at least, of the meaning of the various elements we meet with in it.

The leading part must unquestionably be assigned to the pyramidal cells. From them impulses start, some to the periphery, some to the other grey masses, and some to other regions of the cortex. [Or, as the *translator* would prefer to express it, through them impulses are reflected into efferent channels; the large size of the cell being merely an indication that it is responsible for the nutrition of an extensive fibre-system, and no proof, from the point of view of function, that the largest pyramid is any more important than the smallest granule.] By the division of the axis-cylinder process and the collaterals it gives off, one and the same cell is enabled to conduct the impulses conveyed to it in various directions.

The agents of the transference of impulses to the cells must probably be sought, in the first place, in the ascending fibres (11) which break up and terminate in the cortex. A place of great importance in this connection is probably occupied by the molecular layer, and, more especially, the zonal layer, in which we must look for the terminal branches of the apical processes. *Calleja* has shown that this relation exists in the case of the olfactory cortex (*cf.* p. 334).

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The cortex does not present exactly the same structure in all parts. In some parts the difference affects the number and size of the elements only; in other places the deviation from the type-form which we have described is due to an arrest of development (*tractus olfactorius*, *septum pellucidum*), or to a striking alteration in arrangement (*cortex of cornu Ammonis*).

There can be no doubt that the differences in structure are associated with differences in function. Anatomical considerations, therefore, lead to the conclusion that all regions of the cortex are not functionally equivalent.

It is the exception to find sudden breaks in structure; as a rule, one formation passes gradually into another, at least, in Man and the higher animals. In lower animals (the rabbit, for example) the cortical regions which differ in structure are sharply marked off from each other (*Bevan Lewis*).

If we move forward from the part of the brain which we have just been describing, namely, the frontal lobe near to the central fissure, we encounter no real change in structure, although as we approach the **frontal pole** the large pyramids become smaller. In the anterior central convolution some of these cells are of remarkable size. The zonal layer increases in breadth at the same time.

The higher we mount towards the great longitudinal fissure on the central convolutions the larger do we find these cells to be; they reach their maximum size (65  $\mu$ ) in the **lobulus paracentralis**, where they deserve the name of 'giant pyramids' given to them by *Betz*. The third



layer also increases in thickness *pari passu* with the increase in size of the cells. In the **posterior central convolution** large cells are only found near the longitudinal fissure and in the margin of the convolution where it adjoins the fissure of Rolando.

Some points must be referred to in regard to the giant pyramids. They are usually plump in form, not distinctly pyramidal; in size they greatly overtop the other cells, transitional cells being hardly present; they are usually arranged in small groups or nests of two to five, many of the largest being embedded in the layer of small irregular cells. According to Betz, axis-cylinders of striking thickness are found beneath the giant cells, and he supposes that one runs out from the base of each of them. Bevan Lewis thought that the large pyramids were arranged in larger groups, corresponding to the motor areas of the cortex.

[The minute structure of the area of the cortex, stimulation of which produces movements of the muscles, is not sufficiently different from the structure of the rest of the cortex to allow us to believe that there is any such distinction in function between the two as would justify the appellations 'motor' and 'sensory' areas. The histologist, as far as he is able to draw conclusions as to function from his observations of structure, is bound to say that the grey matter all over the great brain contains elements suitable for receiving the terminations of afferent, and forming the starting-points (trophic centres) of efferent fibres. Small cells (granules) and full-bodied cells (pyramids) are everywhere present. The differences between the several regions depend upon the number and distribution of the former rather than upon the size of the latter. The pyramids found in the limb- and trunk-areas are larger than those occurring elsewhere. If it be true that, other things being equal, the size of a cell varies as the length of the fibre over the nutrition of which it presides, the differences in size of the pyramids of the cortex may be explained by remembering that in the area just mentioned the pyramids are the starting-points of long fibres which traverse the spinal cord; while the fibres which go to the muscles of the face, eye, ear, etc., are much shorter.

In the occipital cortex, especially of the cat and some other animals, very large pyramids occur at intervals. They strongly suggest that afferent visual impulses originate direct cortical messages for the limbs rather than indirect messages transmitted *via* the 'motor area.']

The part of the occipital cortex about the fissura calcarina presents striking peculiarities of structure, evident even in a fresh brain when examined by the naked eye. In the midst of the grey substance we see (in the human brain) a sharply-defined white stripe, Gennari's or Vicq d'Azyr's stripe (ruban de Vicq d'Azyr), which is analogous to Baillarger's (outer) stripe in other regions of the cortex.

Meynert distinguished eight layers in this part of the cortex. The distinction is, however, somewhat forced in the cross-section, and consequently more recent observers do not adhere to his eight-layered type.

The molecular layer is somewhat thinner than in other parts of the



brain surface, but very rich in fine tangential fibres, and a great many Cajal's cells are said to occur in it. The cells of the second layer are present in great abundance. They deviate widely from the pyramidal type, especially in the upper layers, and hence *Ramón y Cajal* assumes the existence of a distinct layer of vertical spindle-cells. These cells have one protoplasmic process directed outwards, similar in behaviour to the apical processes of other small pyramidal cells, and another which courses downwards without dividing until it reaches the neighbourhood of Gennari's stripe, and there gives off a descending axis-cylinder process.

*Ramón y Cajal's* observations on this subject were made on the brains of small mammals, and the results must, therefore, not be transferred, as a matter of course, to the human brain; the less so as any attempt to homologise the cortical regions in animals and in Man must be made with the greatest caution.

About the border between the large and small pyramidal cells the interweaving of nerve-fibres is remarkably close, giving rise to the appearance of Gennari's stripe. A little below it (or sometimes a little above) the pyramids increase slowly in size, much more slowly than in the frontal lobe, for example. On the other hand, in the deepest parts of this layer, and below it, pyramids of remarkable size are found singly (*Meynert's* solitary cells), or in groups. Numerous polymorphous cells lie in the deepest layer, which was subdivided by *Meynert* into several layers. *Flechsig* finds a structure precisely similar, though less pronounced, in the gyrus temporalis superior.

The **gyrus fornicatus** does not throughout its whole course represent the real border of the cortex, but leads up to it both in the portion (gyrus cinguli) which lies above the corpus callosum and farther on in the gyrus hippocampi (subiculum cornu Ammonis).

The cortex of the **gyrus cinguli** is about 3 mm. broad on its peripheral side (fig. 195), but it narrows as it approaches the corpus callosum to about 1 mm.; finally, where it rests upon the corpus callosum, the sulcus corporis callosi (or, as it has also been termed, ventriculus corporis callosi, Sabatier's ventricle, arcuate fissure) intervening, the cortex mantle appears to be sharply cut off. As a matter of fact it is continued medianwards over the surface of the corpus callosum as a very thin layer (20 to 30  $\mu$  thick), the indusium griseum corporis callosi, *Jgr*, which rises into a ridge 0.3 to 1.0 mm. high, *Stlm* (stria longitudinalis medialis, nervus Lancisii). The most lateral part of the indusium, usually a little thickened, is designated the ligamentum tectum (stria longitudinalis externa seu lateralis seu obtecta).

The cortex of the gyrus cinguli presents nothing characteristic in its first two layers. The third layer contains for about its outer half only small pyramids; in its inner half pyramids almost all of the same medium size (about 25 to 30  $\mu$ ). They lie, for the most part, at the bottom of the third layer where it adjoins the fourth; so that between them and the small pyramids is situated an intervening layer, with few cells, distinctly striated by the traversing apical processes of the large pyramids (stratum



radiatum). Next comes the layer of the small irregular cells, not distinctly arranged in columns; and, lastly, an inconspicuous fifth layer. The narrowing of the cortex occurs principally at the expense of the third layer, the larger pyramids becoming more and more scarce and finally disappearing. By the time the fibres of the corpus callosum break through it, the second and fourth layers of the cortex are already fused together.

Compared with other convolutions, the gyrus cinguli is remarkably poor in nerve-fibres; the plexus externus is broader, but less close than in other parts of the brain cortex; and in the deeper layers also the nerve-fibres are more loosely interwoven (*Greppin*).

Single nerve-cells of small size can be found occasionally in the ligamentum tectum. They are met with in larger numbers in the stria longitudinalis medialis. In this band a deeper layer of grey substance containing small irregular nerve-cells and a peripheral layer rich in medullated nerve-fibres, representing the tangential border-zone, may be distinguished; the stria owes its white colour to the latter, that is to say to the longitudinal fibres which course beneath the actual grey layer, and constitute the medullary centre of this rudimentary part of the cortex.

Thus we see that we have to look for the real edge of the cortex-mantle in the stria longitudinalis medialis, with the fascia dentata (outer arcuate convolution). In front the stria longitudinalis medialis passes over into the mesial frontal convolution (*cf.* fig. 160) and the pedunculus septi pellucidi; behind, it passes not only into the fascia dentata cornu Ammonis, but also into the white layer which we have already met with under the name substantia reticularis Arnoldi.

In many respects, but especially as regards its third layer, the cortex of the subiculum cornu Ammonis has an obvious likeness to that of the gyrus cinguli. We will discuss the subiculum in connection with the cornu Ammonis itself, up to which it leads.

The **parietal lobe** or region lying behind the posterior central convolution is characterised by a thickly-packed layer of small pyramidal cells, which is intercalated between the third and fourth layers (*Bevan Lewis*). These cells must not be confounded with the small variously-shaped cells of the deeper layers.

The cortex of the **convolutions of the island of Reil** does not depart from the ordinary type (*Herbert C. Major*). *Mondino* drew attention to the spindle-cells which lie in it, especially in the depths of the sulcus marginalis posterior insulæ, and send out richly-branching dendrites which run parallel to the surface and form a sharply-defined boundary between the grey cortex and the medullary substance. *Meynert* is of opinion that the claustrum ought to be included with the cortex, since it contains fusiform cells, which correspond in form and size with the cells of the usual fifth layer ('claustral formation'); they are disposed, for the most part, parallel with the surface. These fusiform cells are found chiefly in the marginal parts of the claustrum; in the inner layers cells of various shapes, all approximating more or less to the pyramidal type,



preponderate. For this reason, more recent observers have rejected *Meynert's* theory. *Mondino* sees in the claustrum merely the continuation and end of the cortex of the temporal pole, which here extends into the medullary substance. Between the claustrum and cortex proper lies a layer of white fibres (lamina fossæ Sylvi), which is thin beneath the fissures, broad under the summits of the convolutions.

In the **nucleus amygdaleus**, which lies beneath the uncus, the same cells are to be found as in the cortex. The majority of the scattered irregular nerve-cells found here approximate to the pyramids in shape, and it is beyond question that in the nucleus amygdaleus we have a modified and thickened portion of the temporal cortex. I have already pointed out that this region is probably connected with the olfactory nerve; although *Mondino* and others deny the existence of any connection between the tractus olfactorius and nucleus amygdaleus. [The nucleus amygdaleus is directly continuous with the claustrum.]

To *Hammaberg* we owe the most exact comparison of the number, size, and disposition of the nerve-cells in the various parts of the cortex; the variations of behaviour among the nerve-fibres of different cortical regions can be best studied in the works of *Kaes*.

We have still to mention three regions in which the structure is obviously peculiar.

(1) We have already given an account of the atrophied cortex of the **tractus olfactorius** (p. 330).

(2) The **septum pellucidum** is that part of the wall of the cerebral vesicle which was cut off from the general surface by the development of the corpus callosum. It is of scarcely any importance functionally, and in structure is also exceedingly rudimentary. Sometimes the septum pellucidum, together with the ventriculus septi, extends as far back as to the splenium, completely separating the fornix and corpus callosum. In early stages of development this arrangement is the rule.

The part of the lamina septi, which looks into the ventriculus septi pellucidi, corresponds with the free surface of the cortex. It is not, like the real ventricle walls, covered with epithelium, but by a distinct, although thin, superficial layer rich in medullated nerve-fibres, corresponding to the tangential border-zone. Next to this comes a grey layer containing a good many nerve-cells. Nearer to the fifth ventricle the cells are distinctly pyramidal, and provided with an apical process directed medianwards—i.e., towards the surface, corresponding to the free surface of the rest of the cortex. In the deeper layer the cells are irregular. Towards the lateral ventricle the septum presents a layer of medullated fibres, covered with the usual ventricular ependyma. The spaces in the septum for vessels are most of them remarkably wide. Often the lamina septi is not so well developed as this, and the distinction of the several layers is then very difficult. In many animals the septum pellucidum is far less reduced than in Man, and a larger number of better-developed cells can be distinguished in it. Sometimes the two laminae grow together so closely as to prevent the formation of the ventriculus septi pellucidi. This



is the case in the mouse, rabbit, pig, cat, and dog; in the calf, sheep, and horse, the conditions are the same as in Man.

(3) The **cortex cornu Ammonis**. We have already explained how as we advance into the lateral ventricle through the sulcus hippocampi we come across the following structures, each placed longitudinally:—Subiculum cornu Ammonis (gyrus hippocampi), fascia dentata, fimbria, and then the proper cornu Ammonis, lastly the unimportant eminentia collateralis Meckelii.

[While above the corpus callosum the margin of the cortex (where it is pierced by the corpus callosum and by the crura cerebri coming up to the great brain from the brain-stem) is thick, blunt, and uniform (except for its prolongation as the indusium), the continuation of the margin where it bounds the 'porta' on the lower side is peculiarly disposed. Almost as soon as the margin of the cortex passes over the corpus callosum, it becomes considerably thinner and folds upon itself, first outwards and then inwards again. It is this thin folded edge of the cortex which constitutes the cornu Ammonis (hippocampus). The extreme edge of the mantle is again thickened into a ridge and received into a special sheath of grey matter, the fascia dentata. The internal white lining of the hemisphere where it meets the external grey covering is also thickened into a ridge, the fimbria.]

The part of the gyrus hippocampi, which adjoins the gyrus occipitotemporalis lateralis, shows a cortex structure deviating but little from the ordinary type. But as soon as the convexity of the gyrus hippocampi is reached, changes make their appearance, which become more conspicuous as the fascia dentata is approached, and are the precursors of the proper cornu Ammonis (figs. 196, 200, and 201).

The molecular layer is very much broader; the increase in thickness being due chiefly to a great development of the peripheral medullary zone (lamina medullaris externa, *Lme*, fig. 200). The thickening is not uniform; the superficial layer of medullated fibres forms a succession of prominent ridges projecting into the cortex, with valleys between (fig. 196). This varying thickness of the medullary covering is the cause of the easily recognisable reticulated white marking of the region in many fresh brains. The superficial fibres run 'tangentially' as in other parts of the cortex, and are therefore exposed in length in transverse sections. The chief mass of the medullated fibres, upon which the considerable thickening of the layer depends, is disposed horizontally from before backwards.

From the superficial medullary layer, especially from its eminences, a rain of medullated fibres pours into the more deeply-lying medullary substance.

The nerve-cells are not arranged in a symmetrical sheet in the layer of small pyramids; rather do they form a chain of hills, each resting with its base upon the deeper part of the cortex, while its apex is received into one of the valleys of the superficial layer. From this description it follows that a real molecular layer hardly exists, for it is almost entirely occupied by longitudinal medullated fibres.



Cells of the smaller sort, transitional between the second and third layers, are almost entirely wanting in the third layer, just as in the gyrus cinguli. It contains hardly any but large pyramids with very conspicuous long apical processes. The largest pyramids in the deepest part of the stratum are about  $40\ \mu$  in length.

The radial bundles of medullary fibres already mentioned run parallel with the apical processes throughout the whole layer (stratum radiatum), and, combined with the lack of any large number of cell-elements, give it a striking radial striation. Besides these, however, many longitudinal fibres, some coarse, others fine, which run in the direction of the convolution, are cut across in this layer. They give a curious spotted appearance to the section, visible even in carmine preparations. The fourth and fifth layers are fused into a thin sheet

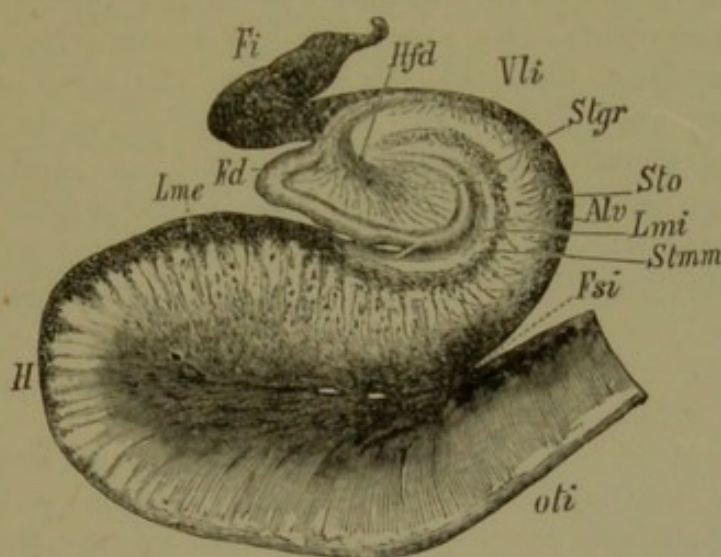


Fig. 200.—Transverse section through the cornu Ammonis. *Pal's staining. Magn. 4.*—*H*, Gyrus hippocampi; *oti*, fissura occipito-temporalis inferior; *Fsi*, fissura subiculi interna; *Lme*, lamina medullaris externa; *Fd*, fascia dentata; *Fi*, fimbria; *Vli*, descending horn of lateral ventricle; *Stmm*, stratum medullare medium; *Lmi*, lamina medullaris interna; *Alv*, alveus; *Sto*, stratum oriens; *Stgr*, stratum granulosum; *Hfd*, hilum fasciæ dentatæ.

which contains, almost exclusively, small irregular cells embedded in a close network of nerve-fibres which twist about in the most varied directions, but lie (especially as the medullary centre is approached) longitudinally for the most part.

The cornu Ammonis proper may be considered to commence at the place where the vascular pia mater grows to the cortex of the subiculum. Whilst the subiculum presents, as seen in cross-section, an arch of cortex with its convexity towards the middle line, the cornu Ammonis is joined to it as an arch with its convexity directed outwards into the inferior horn of the lateral ventricle, *Vli*.

In the cornu Ammonis, in preparations made according to Weigert's method, a three-fold layer of medullary fibres is shown.

The lamina medullaris externa splits into two; one of these layers is simply the superficial medullary layer of the cortex remarkably



thickened, *Lmi* (nuclear layer, lamina medullaris involuta). Its fibres run in the plane of the section when cut transversely. The other layer derived from the lamina medullaris externa of the subiculum is also rich in medullated fibres, *Stmm* (stratum medullare medium). It lies parallel to the nuclear layer, but its nerve-fibres run for the most part obliquely or longitudinally from before backwards.

The third layer of the cornu Ammonis, *Alv* (alveus), covers the surface which is directed towards the inferior cornu of the ventricle. It is the continuation of the central white matter of the subiculum thinned out to cover the cornu Ammonis.

The alveus proper consists of bundles of fibres closely packed together and interwoven in a complicated manner. On its deep surface, towards the cortex of the cornu Ammonis, that is to say, the alveus is resolved into a layer of fibres not united into bundles, but running principally in arches parallel to the curvature of the cornu Ammonis (stratum oriens of Meynert).

In the transition from the subiculum to the cornu Ammonis the nerve-cells behave as follows:—The hills of small pyramids become fewer and lower, and at last these cells of the second layer disappear; as the smaller cells are lost the large pyramids retire to the deepest stratum only of the third layer [where they constitute a uniform sheet, little more than one cell thick]; the fourth and fifth layers of cells disappear almost completely.

The following layers are now to be distinguished in the cornu Ammonis (fig. 201):—

(1) Nuclear layer, *Lmi*—this layer is separated from the fascia dentata for a short distance by the fold of pia mater; farther on the two layers fuse together. Fusiform cells are to be found scattered amongst the nerve-fibres. This medullary layer is homologous with the zonal tangential layer.

(2) The stratum moleculare, *Stm*, reaches to the stratum medullare medium, and is constituted like the layer of the same name in the typical cortex.

(3) Stratum lacunosum, *Stl* (stratum reticulare *seu* medullare medium), may be supposed from its position to correspond with the layer of small pyramids. Its tissue is singularly loose; a good number of capillary vessels, made more conspicuous by the large spaces in which they lie, make an obvious network. The behaviour of the numerous medullary fibres in this region has already been described. A few small irregular nerve-cells are also found in this layer.

(4) Stratum radiatum, *Str*. The apical processes of the large pyramids of the next layer produce a marked striation of this stratum, which is the more distinct owing to the almost complete absence of cells. It represents the outer part of the layer of large cells in the cortex, in which, however, the pyramidal cells are wanting.

(5) Stratum cellularum pyramidalium, *Stp*, is made up of large pyramids of almost uniform size ( $40\ \mu$ ) in close order.

(6) Stratum oriens, *Sto*; scattered fusiform cells, representatives of



the cells of the fifth layer of the cortex, lie amongst the medullated fibres.

(7) Alveus, *Alv*, the actual medullary centre of the cornu Ammonis.

(8) Towards the ventricle the alveus is covered by a rather thick ependyma, *E*, with the usual form of epithelium.

On to the convexity of the cornu Ammonis two terminal structures are fixed (fig. 200), the one, the fimbria, composed entirely of medullated fibres with thick gleial septa; the other, the fascia dentata, made up for the most part of grey matter.

**Fimbria**, *Fi* (bandelette de la voûte), is in immediate connection with the alveus proper; it consists of thick bundles of longitudinal fibres [and passes into the posterior pillar of the fornix].

**Fascia dentata**, *Fd* (toothed ridge, corps godronné), represents the real edge of the cortex [from which it is so sharply defined, and differs so much in structure, that it may be supposed to be a kind of grey matter not elsewhere present in the cortex, but added to its margin in this situation]. It squeezes itself into the concavity of the cornu Ammonis, with which in some places it grows together, as described above.

The fascia dentata is a much-modified part of the cortex. Where it is embedded in the curve of the cornu Ammonis and unites with it, the superficial layers of these two portions of cortex are in contact (*cf.* figs. 200 and 201); a circumstance which may at first add a difficulty to the full understanding of this region.

Here (fig. 201) we find two kinds of nerve cells:—(1) A narrow layer parallel with the surface of the fascia dentata, *Stgr* (stratum granulosum seu corporum nervorum arctorum), made up of closely-packed cells of a rounded angular or pyramidal shape; as a rule, the nuclei are surrounded by so little protoplasm that they might be considered as 'granules.' Hardly any ground-substance is left between these cells. The arch formed by this layer as seen in transverse sections is open towards the fimbria at the 'hilum.'

(2) The second kind of nerve-cells which we meet with in the fascia dentata, correspond to the large pyramids of the cornu Ammonis; they are dispersed with an irregular stratification throughout the whole of the space enclosed by the stratum granulosum.

The fascia dentata shows the following layers, therefore:—

(1) A distinct superficial sheet of medullated fibres (stratum marginale), the continuation of the nuclear layer, but far thinner than the latter. This layer is not distinct in carmine preparations, especially when but slightly magnified; it is, therefore, not represented in fig. 201; it should be looked for at the spot where the lamina medullaris interna and the cornu Ammonis grow together.

(2) Stratum moleculare, *Stmf*.

(3) Stratum granulosum, *Stgr*.

(4) The nucleus fasciæ dentatæ, *Stpf* (layer of pyramidal cells). The cells, as well as the arched fibres of the stratum oriens, enter through the hilum and scatter in all directions. [They are continuous with the



sheet of pyramidal cells of the subiculum cornu Ammonis, and belong therefore to the ordinary cortex rather than to the fascia dentata.]

The fascia dentata is so unlike other parts of the cortex in structure that it is difficult to homologise the several layers. The superficial medulla would roughly correspond to the zonal layer in the typical cortex; the stratum granulosum to the layers of small and large pyramids; the deeper layers would be wanting; while the large pyramids of the nucleus would have to be regarded as cells insinuated from the cornu Ammonis. *Hill* is therefore of opinion that the fascia dentata should not be looked upon as the final margin of the cortex, but that we should see in it a peculiar kind of grey substance, not found elsewhere, and here added on to the free edge of the cortex, which, as the so-called nucleus fasciæ dentatæ, rolls over, to be received by the reversed fold of fascia. [The

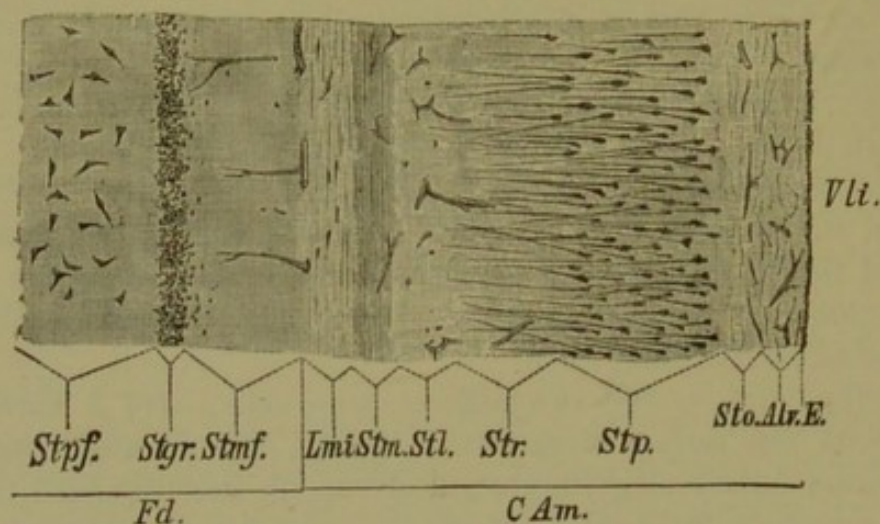


Fig. 201.—Cortex of the cornu Ammonis and a part of the fascia dentata. *Magn.* 20.—*CAm.*, Cornu Ammonis; *Fd.*, fascia dentata; *Vli.*, inferior horn of the lateral ventricle; *E.*, endyma; *Alv.*, alveus; *Sto.*, stratum oriens; *Stp.*, stratum cellul. pyramid.; *Str.*, stratum radiatum; *Stl.*, stratum lacunosum; *Stm.*, stratum moleculare; *Lmi.*, lamina medullaris interna; *Stmf.*, stratum moleculare fasciæ dentatæ; *Stgr.*, stratum granulosum; *Stpf.*, stratum of pyramids beneath the fascia dentata.

fact that the fascia dentata varies directly in amount with the olfactory apparatus seems to point to its being the fore-brain end of the organ, which, at its anterior extremity, constitutes the olfactory bulb. The *translator* has shown that in the cetacea in which the olfactory bulb is absent the fascia dentata also is totally absent.]

Farther forwards the fimbria grows progressively smaller; on the other hand, the fascia dentata enlarges and sinks at last into the uncus.

As soon as the digitations proper of the cornu Ammonis appear we have to deal with an undulating curved sheet of cortex, covered on its surface by the medullary layer known as the alveus. The fascia dentata, which is always recognised by the quite characteristic stratum granulosum, pushes itself on the under side of the cornu Ammonis into the front part of the fissure hippocampi. Behind, the fascia dentata becomes progressively thinner, until finally it passes round the splenium



corporis callosi as the fasciola cinerea, by which it is continued into its atrophied supra-callosal portion, the stria longitudinalis medialis. Below and in front it emerges from the fissure beneath the uncus and crosses the uncus to its ventricular border as the fasciola unci (band of Giacomini).

In nearly all mammals the cornu Ammonis is relatively larger than in Man. It can be followed far forwards, in connection with the fornix, above the optic thalamus and beneath the corpus callosum. Hence result various histological differences, into which we cannot enter now.

In the foregoing description of the cornu Ammonis we have confined ourselves to such facts as can be learnt from the methods of carmine and medullary-sheath staining. But here, as elsewhere, the method of impregnating with metals has revealed many new and important details. By means of it we perceive that the part which lies nearest to the subiculum, the région hippocampique of *Déjerine*, région supérieure of *Cajal*, differs widely in structure from that which extends to the fascia dentata, région godronnée of *Déjerine*, région inférieure of *Cajal*.

The best-known cells of this region are the large pyramidal cells of

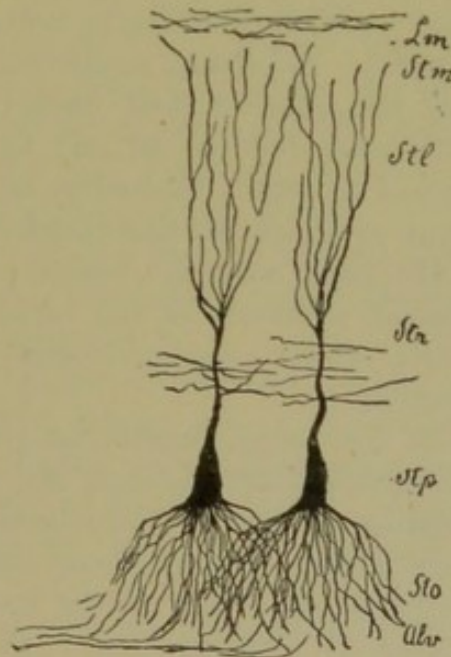


Fig. 202.—Two double pyramids from the cornu Ammonis of a mouse. *Silver impregnation*.—*Lmi*, Lamina medullaris interna; *Stm*, stratum moleculare; *Str*, stratum radiatum; *Stp*, layer of large pyramidal cells; *Sto*, stratum oriens; *Alv*, alveus.

the fifth layer (fig. 202). In the regio hippocampica they are sometimes shaped more like a broad spindle than a pyramid, and are provided with two kinds of protoplasmic processes. The basal processes, or descending dendrites, form an extraordinarily rich close tuft, which passes down into the stratum oriens; the apical process, or ascending dendrite, gives off lateral branches in the stratum radiatum, and likewise breaks up into a tuft of branches, most of which extend upwards as far as the molecular layer. The axis-cylinder process, after giving off some collaterals, reaches the alveus, which it helps to constitute.



These peculiar cells exhibit a striking likeness to the double pyramids in the cortex of the lobus pyriformis.

In the part of the cornu Ammonis which approaches the fascia dentata, these pyramids behave somewhat differently. The cells are larger, the tufts of dendrites shorter and thicker, and the axis-cylinder process enters the fimbria. Near the cell it is said to give off a very large collateral, which takes a backward and upward course to the stratum lacunosum, and there acquires a myelin-sheath in the mesial medullary layer (*Schäffer*).

The other cell-forms which we know in the cortex also occur in the cornu Ammonis, but in much smaller numbers.

The conditions in the fascia dentata are quite peculiar, and stand in need of further investigation.

Many writers suppose that the small cells of the stratum granulosum are modified pyramidal cells, although they differ from the latter in almost every particular.

They possess a number of dendrites, which go off from the cell-body towards the surface (away from the hilum); and an axis-cylinder process which is said to pass out through the hilum, giving off some collaterals in its course, and to proceed horizontally in the pyramidal layer of the cornu Ammonis (*région godronnée*). A prickly, rosette-like growth is said to be visible at intervals along the course of these fibres (with these moss-fibres *cf.* the moss-fibres of the cerebellum, p. 401 and fig. 182). By means of these prickles they are said to attach themselves to excrescences, varicose swellings, etc., in the large pyramids and their dendrites.

In the nucleus of the fascia dentata, besides the large cells which represent the last dispersed pyramids of the cornu Ammonis, we meet with other scattered cells, which may correspond to the various other forms of cells in the cortex.

The type-structure of the cortex mantle, as pictured above, can be recognised with slight modifications through the whole of the mammalian series. The relative number of nerve-cells, their size, and the thickness of the layers which contain them, are variable. On the whole, the size of the nerve-cells varies as the size of the animal. In Man, the molecular layer is relatively thin; the cortex showing a greater wealth of nerve-cells proportional to the increased dignity of this organ (*Meynert*).

In most mammals certain local differences in the structure of the cortex can be exhibited; from a comparison of these with similar variations in the human brain, we may conclude that the parts are functionally equivalent.

In lower mammals the cortex cells are distinguished from those of Man by a difference in internal structure. This difference in constitution is exhibited in their behaviour towards hardening fluids in a way which is not noticed with other parts of the central nervous system, or noticed to a much smaller extent. If, for example, small pieces of the cortex of some rodent animal are prepared by hardening in potassic bichromate, it is found on examination that in place of many of the pyramidal cells the



sections exhibit rounded spaces communicating with the characteristic radiating channels. Cell-nuclei surrounded by irregular, indistinctly-defined finely-granular protoplasm lie in these spaces. The difference from the human type depends upon post-mortem changes, indicating a difference in the chemical constitution of the cells. We find that the cell has come to grief although the brain was placed in the hardening fluid while absolutely fresh, whereas in the case of the human brain such appearances are much more rare, although we must always wait until disintegrative changes have set in before we can harden it.

Similar spaces are seen in imperfectly hardened human brains and in various pathological conditions.

In all animals the cells of the cortex are almost completely devoid of pigment.

In the lower classes of vertebrates the cortex departs widely from the human type; a description of the differences would be out of place in this book.

It is worth noting that in the case of fishes and most amphibious animals the existence of a peripheral layer of cells which can be regarded as a brain-cortex is, to say the least of it, very doubtful. An indubitable cortex is first met with in reptiles, as are also the medullated fibres of the corona radiata (*Edinger*). Philogenetically, the first portion of cortex to appear is the cortex of the cornu Ammonis, which is homologous with the olfactory cortex; and the higher we ascend in the scale the more do the other cortical regions preponderate over it.

The cortex cerebri of the human embryo exhibits numerous round nuclei (formerly called 'gleia-nuclei') which represent the rudiments of the later developed cell-elements.

The nuclei are arranged in successive layers (*Lubimoff* counted six layers in a five months foetus), which in section give the appearance of a series of bands, lighter and darker according to the quantity of nuclei. In the deeper layers the nuclei are arranged in columns, between which spaces are left for the passage of the as yet non-medullated fibres.

The first pyramidal cells are to be seen in the tenth week of intra-uterine life (*Vignal*); for the development of the pyramidal cells of the cortex (see p. 153 and fig. 61). At birth they are very numerous and well formed in the deeper layers (*Lemos*; *S. Fuchs* says in the upper layers also); as are also the giant-cells.

About the same time the first medullated fibres make their appearance in the radiating bundles of the posterior central convolution. Medullated fibres are found in the superficial tangential layers in the fourth month; although the other layers of the cortex are joined to this, the formation in them of medullated fibres seems to be completed not earlier than the seventh or eighth year. It may be asserted that, as a general rule, the fibres first myelinated are those which are subsequently the thickest.



## BLOOD-VESSELS OF THE GREAT BRAIN.

We will only briefly mention here the manner of division of the finer blood-vessels within the cerebrum. The course of the larger vessels and their arrangement, especially on the basis cerebri, will be learnt later on.

It must be accepted as a law for the cerebrum, as for other parts of the central nervous system, that the richer any region is in nerve-cells the closer is the capillary network which supplies it. We still need more exact accounts of the course of the vessels in many parts of the brain.

The application of the law just formulated may be observed in the cortex cerebri (fig. 203). Arteries and veins descend vertically from the

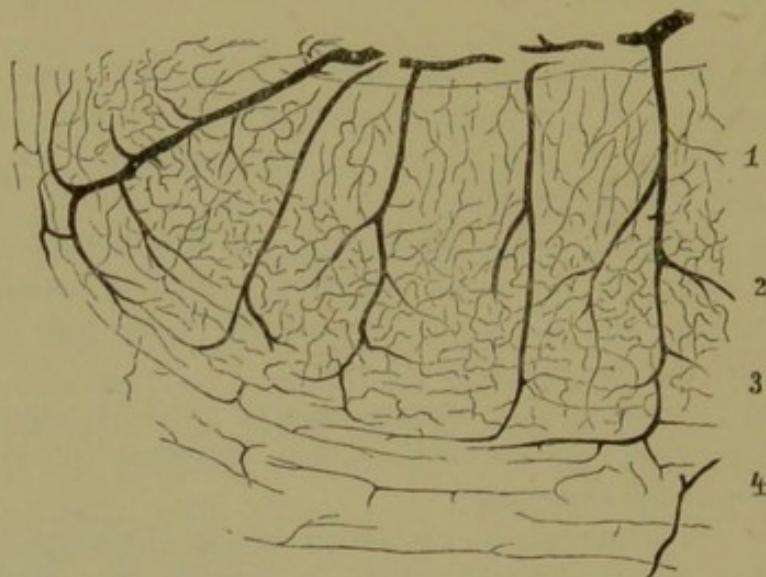


Fig. 203.—Injected cortex cerebri of the dog. *Magn.* 25.—1, The few-celled layer; 2, region of pyramids; 3, the internal (deeper) stratum of the cortex; 4, white substance.

pia mater. The larger ones give off relatively wide lateral branches, and traverse the cortex to reach the medullary centre. The smaller ones are used up in the cortex.

In the cortex at least three kinds of capillary network can be distinguished—

- (1) In the molecular layer it is comparatively wide-meshed, 1.
- (2) A very close net-work in the neighbourhood of the pyramidal cells, 2, which becomes a little looser in
- (3) The deepest cortical layers, 3.

The capillary network, 4, of the medullary substance beneath the cortex is very open, the meshes being placed, as a rule, with their long axes parallel to the surface.

The corpus geniculatum laterale, the corpus subthalamicum, and the nuclei of the nerves, are distinguished from other grey masses by their richness in capillary vessels.



Many anatomical relations are not clearly appreciated, except in injected preparations ; for example, the division of the corpus mamillare into two, in the dog.

## PATHOLOGICAL CHANGES IN THE GREAT BRAIN.

Those life-processes which, in contra-distinction from reflex actions, occur in sight of consciousness, require for their normal course the integrity of a large portion, at any rate, of the cortex. In all diseases in which consciousness is dimmed and the intellect disturbed for more than a very short time, pathological changes may be looked for in this tissue, without reference to the question of the seat of consciousness ; but, as already explained, many of these changes escape our notice on account of our ignorance of the limits of variation of the structural appearances in health of many of the nervous elements, particularly the most important of all—the nerve-cells.

In this place we can only mention the most important pathological accidents to the cortex cerebri which have as yet been described.

In idiocy we are prepared, of course, to find very conspicuous changes in the structure of the cortex. An abnormal disposition of the pyramidal cells has several times been observed, the apical process being turned sideways, or even towards the medullary substance (*Betz, Köster*). *Hannaberg*, it is true, attributes these alleged peculiarities, in many cases at least, to defective observation.

According to the last-named author, we may take for granted that in every case of idiocy the normal development of the cortex has been arrested at a certain stage. As a rule, the development is brought to a standstill only in a small part of the cortex, though it is seriously impeded in the remainder. In such brains the nerve-cells remain, to some extent, in the embryonic condition. A noticeable feature is that in places the pyramidal cells are completely wanting.

The following changes occur in *senile atrophy* according to *Köstjurin* :—

(1) Pigmentary and fatty degeneration of many nerve-cells, perhaps vacuole-formation also.

(2) Diminution in the number of the nerve-fibres in all layers of the cortex.

(3) Atheroma of blood-vessels, as well as overgrowth of the connective tissue in their walls, even to obliteration.

(4) Slight thickening of the gleia-tissue.

(5) Amyloid bodies in the periphery of the cortex.

The cortex behaves somewhat similarly in other slow atrophic processes—*e.g.*, chronic simple lunacy.

After the loss of a limb in infancy, either by amputation or the atrophy consequent upon paralysis, we often meet with changes in the motor region of the contra-lateral hemisphere. The convolutions involved appear narrower, and there is a very marked decrease in the number of



nerve-cells (*Sibut*). Here we have to do, of course, with simple atrophy from loss of function.

Congenital deafness, on the other hand, may often be referred to more or less severe atrophy of the gyri temporales superiores on both sides. In such cases the peripheral auditory nerves and the central auditory apparatus seem to remain intact as far as the internal corpus geniculatum (*cf.* p. 369).

In DEMENTIA PARALYTICA we have under observation a peculiar form of atrophy of the brain. In spite of numerous investigations of the subject, two views concerning the genesis of the process still stand in sharp antagonism. According to the opinion of a great number of observers, we have here to do with a parenchymatous process, a primary destruction of the nerve-cells, and then of the medullated fibres of the cortex. As a secondary process, perhaps, an overgrowth of gleia takes place, to fill in the vacant spaces. According to the other view, the essential process is a diffuse primary sclerosis of the cortex, which leads to atrophy. It makes itself felt in the frontal lobe first. The sclerosis is preceded by a condition of irritation which seems to justify the expression *periencephalitis chronica*. It is in the overgrowth of the cells belonging to the gleia that we have to look for the cause of the sclerosis. As soon as these new cells occupy so much space as to surround and press upon the normal nerve-tissue cells, the latter atrophy. The result of this process is seen in old-standing cases, not only in the degenerated nerve-cells (especially fatty-pigmentous degeneration, sclerosis of the cells, and enlargement of the pericellular spaces), but also in the remarkable diminution in the quantity of medullated fibres (*Tuczek*). This disappearance of medullated fibres advances from the periphery inwards; so that, as a rule, the outermost layer of tangential fibres is most affected, whereas in senile atrophy the decrease in the number of fibres affects all the layers equally, and none so greatly as in this disease. If we give in our adherence to the theory of an interstitial disease of the cortex, this is most easily explained on the supposition that the tangential fibres of the zonal layer are the first to suffer from the overgrowth of the submeningeal gleial stratum. This explanation would also serve for the growing together of the cortex and the meninges. It will not do to assume, with *Wernicke*, that this last is merely a post-mortem appearance, for, if it were so, we should meet with the same condition in healthy brains under the same circumstances.

The actual intra-cortical medullated fibres come to grief after the zonal fibres, and the bundles which stream in radially are indirectly affected. According to *Tuczek*, the convolutions most constantly and distinctly affected are those on the orbital surface of the frontal lobe, especially on the side of the great longitudinal fissure; next those of the island of Reil, and the left inferior frontal convolution. The other frontal convolutions, the gyrus fornicatus and the superior temporal convolutions, are likewise often diseased. All other parts of the cortex are, it is supposed, affected in a less degree only, or not at all (occipital lobe,



lobulus paracentralis). The diseased nerve-fibres appear at first strongly varicose, like hypertrophied fibres broken off short and embedded in round granules and masses of detritus (*Greppin*). Hypertrophied axis-cylinders are also found in the brain-cortex of paralysed persons (*Pick*). A decrease in the number of fibres may be met with in other conditions besides dementia paralytica and senile atrophy, all other forms of dementia (*Kéraval*) and long-standing epilepsy for example (*Zacher*).

But we must not ignore the fact that by reconciling these views, and supposing the parenchymatous process to go hand in hand with a co-ordinated interstitial process, we could best explain the character of these changes.

It would be a mistake, however, to seek for the anatomical changes brought about in dementia paralytica in the cortex of the brain alone. Apart from other details, I will only refer to the noticeable reduction of the fibres in the medullary substance of the great brain. Certain kinds of fibres are apt to be peculiarly affected, while others escape more or less completely; thus in diffuse wasting of the medulla we sometimes find the short arcuate bundle quite intact (*Friedmann*). *Lissauer* frequently observed small sclerotic patches in the thalamus opticus. Careful examination of the pathological appearances has shown that the cord is always diseased in dementia paralytica.

A series of cases has been published in which spaces, or veritable CYSTS, have been found within the cortex. They are often found in the brains of those who had died of dementia paralytica. The cause of these hollow spaces is, perhaps, not identical in all cases. Very often they originate in connection with the vessels, being enlargements of the perivascular or adventitial spaces—that is to say, a circumscribed parenchymatous inflammation may also be the cause of the decrease in tissue. In the latter case the cortex cerebri appears from the outside to be unevenly atrophied; on making sections it is seen to be cavernous, the spaces being often occupied, especially in their peripheral part, by a loose connective-tissue network, through which a few well-preserved nerve-fibres still course (*J. Hess*). Single bundles of degenerated fibres are seen deep down in the medullary centre in situations corresponding to the foci of cortical disease (fig. 204).

EFFUSION OF BLOOD into the great brain is very common; capillary effusions are met with in the cortex. These may be so numerous and close together as to stain an extensive cortical area reddish-brown. Several forms of disease of the intra-cerebral vessels lead to rupture. Alterations in the muscular coat (fatty and granular degeneration, etc.) are especially important. Rupture is also due to alterations of the intima, such as atheroma; the atheromatous patches, becoming detached, block vessels further on, and as the result of the embolism the vessel wall is ruptured.

Very often, but not always, miliary aneurysms are found in the tissue surrounding large cerebral apoplexies. Every effusion, whether large or small, spreads out in the direction in which it encounters least



resistance. All apoplectic lesions are transformed eventually into apoplectic cysts or cicatrices.

The formation of new vessels of the finest possible calibre is asserted to have been observed in cases of dementia paralytica (*cf.* p. 183).

Patches of DISSEMINATED SCLEROSIS may be found anywhere in the brain; but they are not so common or so extensive elsewhere as they are in the walls of the lateral ventricles. Sometimes the brownish gelatinous degeneration is seen to surround the whole ependyma of the ventricle so far as it rests on white substance. They are less common in the cortex than in the medullary substance. Histologically their leading characteristic is the overgrowth of gleial tissue. *Gowers* terms very small patches of sclerosis which are arranged in the deepest layer of the cortex, MILIARY SCLEROSIS.

A very peculiar form of SCLEROSIS is LIMITED TO THE CORNU AMMONIS, in which this structure becomes as hard as cartilage and

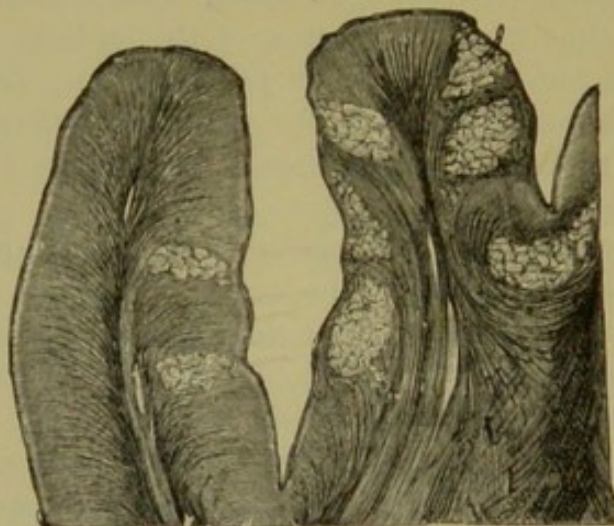


Fig. 204.—Encephalitic cysts of the cortex cerebri with secondary degeneration of the white substance. *Weigert's colouring. Magn. 4.*

much shrivelled. This form of sclerosis is almost restricted to epileptics; it is present in more than half of all the cases of epilepsy (*Pfleger*); it may be uni- or bilateral; the left side is that most commonly affected. An examination of other parts of the cortex of epileptics is said frequently to reveal slight sclerosis of this sort, due to an overgrowth of gleia. It chiefly affects the motor region, but may be found in any part of the cortex cerebri (*Chaslin*).

A DIFFUSE SCLEROSIS of the brain due, in part at any rate, to overgrowth of the interstitial gleia-tissue may be almost equally distributed over the two hemispheres. As the result of this process the brain becomes as hard as leather and almost like cartilage in appearance. It is a rare form of sclerosis; occurring most often, perhaps, in idiot children.

INFLAMMATORY PROCESSES in the brain may have different causes. That form of encephalitis which leads to the formation of abscesses is usually the result of external injuries or else is due to the spread of purulent



inflammation from surrounding structures (caries of the temporal bone especially). Metastasis of abscesses from distant organs, and especially from gangrenous disease of the lung, is not rare. In pyæmia, especially when puerperal (*Rokitansky*), numerous little metastatic abscesses from the size of a grain of hemp up to that of a bean are occasionally formed. Embolic and thrombotic softenings are classed with the inflammatory processes in the brain. The various kinds of bodies which may lead to embolism of the arteries of the brain have been already enumerated (p. 184). In certain acute infectious diseases, *e.g.*, splenic fever and variola hæmorrhagica, very numerous effusions of blood may make their appearance in the brain substance and in the pia mater. They are probably caused by accumulation of the infective medium in small heaps in the vessels, resulting in embolism. The large vessels which lie in the pia mater outside the brain-substance proper, at the base, and elsewhere, are also subject to embolism, in the production of which other causes come into play. The emboli for the larger vessels come, as a rule, from the left side of the heart or from the aorta.

The thrombus is usually a patch of atheromatous or of syphilitic inflammatory substance formed in the intima. In regions in the brain in which, owing to occlusion of the blood-vessels, necrosis of nervous tissue has ensued, very numerous capillary hæmorrhages often occur (red softening); later on the blood pigment is taken up by innumerable fat-granule cells (yellow softening). Sometimes no colouring of the lesion by blood pigment is noticeable (white softening); but in that case the fat-granule cells are more or less crammed with the remains of the medullary investment of the nerves. Softened patches are often found in the cortex as the result of meningitis tuberculosa; they lie beneath much diseased spots in the pia mater and often stretch into the medullary substance.

TUMOURS of the brain are very common; sometimes they originate in the membranes, sometimes in the brain-substance. Peculiar to nervous tissue is the form of tumour termed glioma, in the formation of which nerve-cells, as well as other tissue-elements, probably take part (*Fleischl, Klebs*). Pure glioma is, however, rarer in the brain than mixed forms. Gummata and solitary tubercles are very frequent, so too are sarcomata of the most varied kinds; cylindroma is less common; melano-sarcomata are not rarely observed; but neither carcinoma nor sarcoma, perhaps, ever has a primary origin in the brain. Myxomata have been repeatedly seen; so have osteomata. Concretions which may occasionally form small psammomata are not rare in the ventricular ependyma. Metastatic tumours are very apt to develop in the brain after the corresponding disease in the lungs.

Cysticerci coming out from the pia mater often in great numbers take up their seat in the cortex. Free cysticerci sometimes occur in the ventricles of the brain, and may give rise to hydrocephalus internus, or to softening or granulation of the ependyma. Echinococcus-vesicles and dermoid cysts are very rare.



The clumps of grey substance which are sometimes found within the medullary centre must not be looked upon as tumours; in minute structure they resemble the neighbouring grey masses or the cortex. They are termed heterotopes, and are most common in the cerebellum. They are always to be traced to abnormalities in development.

To study properly the subtler changes which the nerve-cells of the brain-cortex undergo from the effects, acute or chronic, of certain nerve-poisons, we must have recourse to Nissl's method. Some of these forms of degeneration have already been referred to in the account of pathological changes in the nerve-cells (p. 158 *et seq.*). In examining the tissue of the human brain the possibility of post-mortem changes must, of course, be borne in mind. Some have thought that by the silver-method they could detect changes, such as protoplasmatic swelling of the dendrites in lissa (*Golgi*) or alcoholic poisoning (*Lloyd Andriezen, Berkley*); but these observations have been confined, for the most part, to experimental intoxication of animals.

Two structures which are met with attached to the great brain may be now described, the conarium and hypophysis.

(1.) **Conarium** (*glandula pinealis, epiphysis cerebri*). Its connection with the brain is chiefly effected by a bilateral white column of fibres, *pedunculus conarii*. Its connections with the posterior commissure (and so with the oculomotor nucleus and the central visual apparatus) are especially important. It has been proved that the pineal gland is a vestigial structure representing an unpaired eye. In many saurians, especially in *Iguana tuberculata* and *Hatteria punctata*, an organ which corresponds in structure with an eye (parietal or pineal eye) is found lying beneath a thin plate of pigment-free membrane in the parietal region. It is connected by means of a tract of nerve-fibres with the epiphysis. This tract, which is homologous with the optic nerve, has to pass through an opening in the skull (*foramen parietale*) conspicuous by its great size in most fossil amphibia. This arrangement can be clearly recognised in our native lizard (*Lacerta agilis*).

[The fact that in certain reptiles the pineal body resembles an eye in structure was noticed by *v. Graaf*, but credit is due to *Spencer* for appreciating the immense value of this discovery, and systematically examining the pineal body and parietal foramen in all animals in which these structures show traces of their former importance. *Spencer* discovered that, although there is no reason to suppose that it is now functional in any animal (although *Hatteria* can distinguish light from darkness by its means), the pineal eye when best developed exhibits a complicated arrangement of bacillar and nervous elements. Nothing about this prehistoric cyclopic organ is more interesting than the fact that the rods are directed inwards towards the centre of the eyeball as in invertebrates. *Gaskell* has shown that the size, structure, and connections of the ganglion habenulæ in the lamprey indicate that it is the proper ganglion (central grey matter) of the pineal eye.

The nearest extinct ancestors of the saurians in which the pineal eye



may be supposed to have been functional, seem to have been the labyrinthodonts which flourished during the time when the coal measures were being formed.]

The pineal gland receives an enveloping capsule from the pia mater which sends vascular sepiments into the organ.

In sections it is seen to consist of a rather close meshwork of connective-tissue trabeculæ. Numerous cells, seldom larger than  $20\ \mu$ , are found in the alveoli. According to *Bizzozero* two sorts of cells are to be distinguished—one of rounded form with two or three rapidly tapering processes dividing into numerous little branches; the other fusiform, with sharper and more irregular contour; these latter contain yellow or red-yellow pigment-granules, and their processes are more distinct and larger, and end in a fine network. In the pineal gland of the horse, pigment is present in great abundance, both in pigment-glands and epithelial cells (*Flesch*).

Many of the cells of the pineal body, however, show no recognisable processes.

Nerve-fibres are found almost exclusively in the most anterior parts of the organ; nerve-cells have not hitherto been definitely distinguished. A peculiarly close interweaving of neurogleia is said to take place in the inner and lower division (*Weigert*).

[In the pineal glands of young persons, as in the cerebral part of the pituitary body, little can be recognised under the microscope but a granular basis with fairly numerous easily stained nuclei, and occasional irregular, usually coiled yellowish fibres.]

In the adult pineal bodies, concretions of phosphate and carbonate of lime (brain sand, acervulus) are often found. They are small stratified bodies arranged in nodules, resembling mulberries in form; the nodules may be as large as hemp-seeds. Rod-like and club-shaped or branched pieces of calcified connective tissue are also to be found in the conarium. These concretions seem to be quite wanting in animals, although in the horse they may be replaced by very fine granules of phosphate of lime (*Faivre*).

(2.) **Hypophysis** (glandula pituitaria, appendage of the brain, colatorium) is a body about as large as a bean, somewhat less in its sagittal than in its frontal diameter. It is connected with the rest of the brain by the infundibulum.

A sagittal section shows that the apparently single body [is invested with a thick capsule of dura mater, and] is composed of two distinct divisions; the anterior lobe (epithelial portion, hypophysis proper) is shaped somewhat like a heart and is larger than the posterior lobe (cerebral portion, lobus infundibuli, conical lobe), which is spherical.

The ANTERIOR LOBE is composed of alveoli, surrounded by connective-tissue membranes, and containing two different kinds of cells, the larger of which stain more strongly with hæmatoxylin than the other or smaller kind (*Flesch*). Numerous wide blood-vessels with extremely delicate walls run between the gland-pits. A number of these gland-pits creep up the anterior wall of the infundibulum towards the base of the brain.



A cleft, concave towards the back, does not, as might be supposed, separate the two lobes of the hypophysis, but falls entirely within the epithelial part. It is not constant in Man.

Both the gland-follicles and the blood-vessels frequently contain colloid substance. It is also not seldom found in the inter-follicular connective tissue, where it sometimes forms larger colloid cysts.

The spaces in the connective tissue are supposed to be lymph-spaces (*Pisenti* and *Viola*). It is also asserted that an increase in the colloid masses in the hypophysis takes place in struma.

Fine nerve-fibres, belonging to the sympathetic nerve, are said to be present in this, as in other glandular organs (*Berkley*).

[The epithelial character of the cells is very evident. Their round vesicular nuclei, firm homogeneous yellowish cell-bodies, often vacuolated or containing droplets of fat, and destitute of cell-wall, their polyhedral shape and grouping in alveoli, all tell of their origin, and recall to the histologist other organs made up of apparently functionless epithelial cells, such as the cortex of the supra-renal capsule, corpora lutea, &c.] The anterior lobe is formed by an involution of the mucous membrane of the mouth, and is, therefore, homologous with the buccal glands.

The POSTERIOR LOBE must be looked upon as a veritable part of the brain. In it are found bundles of fibres crossing one another in every direction; their histological nature is still doubtful. Most of these fibres exhibit elongated fusiform swellings with longish nuclei, which gives them an appearance not unlike smooth muscle-fibres. Besides numbers of small cells, scattered large pigmented cells are met with, which may certainly be looked upon as nerve-cells, as is more plainly shown by treatment with silver. Non-medullated fibres are found in it, but no medullated nerve-fibres. In the cerebral portions the vessels are less numerous. Most of them are of the calibre of capillaries.

Hypertrophy and tumours of the hypophysis (the glandular portion only) bear an indubitable relation to the inception of acromegaly.

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## SECTION VII.—THE COVERINGS OF THE CENTRAL NERVOUS SYSTEM.

THE whole of the central nervous system is enveloped with a three-fold covering of fibrous membrane.

The outermost coat, or dura mater, *D* (fig. 205), lies within the skull-case, close to the bone, but in the spinal canal [it is not so intimately united to the surrounding bones], although standing at some distance away from the spinal cord. The innermost layer or pia mater, *P*, clings close to the nerve-mass. The middle coat, or

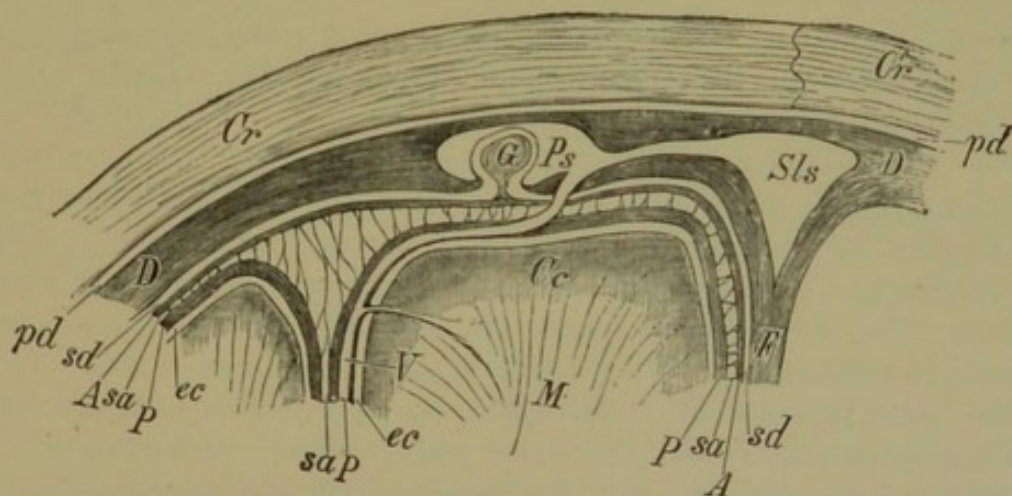


Fig. 205.—Diagram of the membranes of the brain.—*Cr*, Cranial bones; *pd*, peridural space; *D*, dura mater; *F*, falx cerebri; *sd*, subdural space; *A*, arachnoid; *sa*, subarachnoidal space; *P*, pia mater; *ec*, epicerebral space; *Cc*, cortex cerebri; *M*, white matter of the brain; *Sls*, sinus longitudinalis superior; *Ps*, parasinoidal space; *G*, glandula Pacchiona; *V*, veins of the pia mater.

arachnoidea, *A*, lies everywhere close inside the dura mater, touching it in many places; but only united to it by scanty threads of connective tissue. To the pia mater, from which in many places it is separated by a considerable space, it is tied by a great quantity of connecting plates and filaments (subarachnoid tissue), especially around the brain. So abundant are the connections that pia and arachnoid are often mistaken for a single membrane.

Two spaces are confined between these three membranes; the



subdural space, *sd* (or arachnoidal sac), between dura and arachnoidea the subarachnoid space, *sa*, between arachnoidea and pia mater.

Owing to the close proximity of the arachnoid and the dura, the SUBDURAL SPACE is very narrow, and contains but little fluid. *Schwalbe's* investigations seem to have proved that it is a lymph space. Colouring masses injected into the subdural spaces enter the lymphatic vessels and glands of the neck, and the lumbar lymphatic glands, as well as the subdural spaces around the nerve-roots. From the lymph spaces around the nerve-roots the injection-mass travels on into the lymphatic space in the olfactory membrane, in the labyrinth of the ear, and in the bulbus oculi (perichoroidal space). All these channels do not seem to exist in Man; at any rate it cannot be proved that the lymphatics of the neck are in direct communication with the subdural space. There is no communication between the subdural and subarachnoid spaces. *Langdon* professes to have found, near the flocculus on either side, a crescent-shaped cleft in the arachnoidea at the point where it passes over from the medulla oblongata to the cerebellum.

Owing to the peculiar configuration of the brain the SUBARACHNOID SPACE is divided into a considerable number of larger and smaller spaces, which communicate with one another, and, through the foramen of Magendie and the aperturæ laterales ventriculi quarti, with the ventricles of the brain.

*Merkel*, as well as *Mierzejewsky*, maintain that a slit-like communication exists between the subarachnoid space and the inferior horn of the lateral ventricles (*cf.* p. 68).

The cerebro-spinal fluid (liquor cerebro-spinalis) circulates within the subarachnoid spaces and the ventricles. It finds an outlet in the lymph-paths surrounding the peripheral nerves (particularly the optic and auditory) and beneath the olfactory membrane (*A. Key* and *Retzius*, *Fischer*). The subarachnoid spaces are also, by means of the arachnoid plexuses, in connection with the venous sinuses of the dura mater.

The name epicerebral lymph-space, *ec*, is given to a narrow space supposed to extend around the whole brain between its surface and the under side of the pia. It may, however, be artificially produced, like the space which lies about the spinal cord.

#### A. DURA MATER (coarse or hard membrane of the brain and cord ; Meninx Fibrosa, fibrous membrane of the brain and cord, μήνινξ παχέα).

We distinguish a dura mater cerebialis and a dura mater spinalis. The former of these lies, with the exception of certain prolongations to be mentioned immediately, entirely within the skull-case in close apposition with its inner table; the latter is divisible into two layers, the outer and thinner being the periosteum of the vertebræ, the inner



being the dura mater spinalis, in the strict sense of the word. Between the two laminae, which unite with one another, and with the dura cerebialis at the foramen magnum, little is interposed but plexuses of veins and loose fatty tissue (epidural tissue).

The dura mater cerebialis is a firm white fibrous membrane, which, within the skull-case, gives off several reduplications, viz., the falx cerebri (processus falciformis major), tentorium cerebelli and the inconsiderable falx cerebelli (processus falciformis minor).

To allow of the interposition of the venous sinuses and venous lacunae about to be described, the dura mater is spilt into two layers, the one visceral, the other parietal; the same arrangement obtains, too, wherever nerve-structures such as the trunks of the third, fourth, and sixth cranial nerves or the ganglion Gasseri of the trigeminal (in the cavum Meckelii) are embedded in the substance of the membrane.

It would lead us too far were we to examine in detail the anatomical disposition of the dura mater. We must point out, however, that on

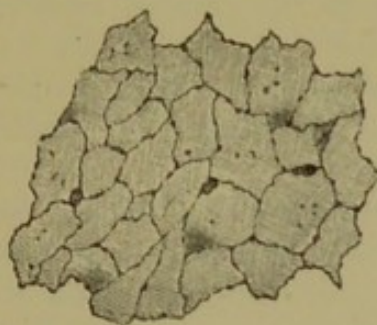


Fig. 206.—Epithelium on the inner surface of the dura mater of the guinea-pig. *Silver impregnation. Magn. 400.*

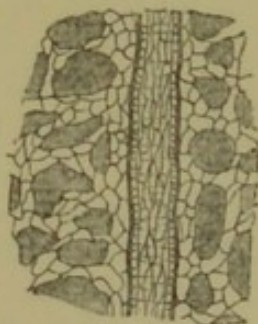


Fig. 207.—Dura mater of a new-born child. *Silver impregnation. Magn. 200.*



Fig. 208.—A corpus arenaceum from the dura mater. *Magn. 300.*

either side the middle line near the sinus longitudinalis superior, *Sl*s (fig. 205), peculiar hollow spaces are met with in the substance of the dura, *Ps* (parasinoidal spaces, lacunae venosae laterales), into which the veins of the brain, *V*, embouch before reaching the sinus.

From twenty to twenty-three triangular plates of connective tissue fix themselves by their points to the inner surface of the dura spinalis, their broad bases resting upon the pia mater along the whole lateral border of the spinal cord (ligamentum denticulatum).

Short isolated threads of connective tissue unite the dura spinalis with the arachnoidea. A constant connection of this sort exists, for example, between the arachnoidea and a point between the anterior and middle third of the falx.

The spinal as well as the cerebral dura forms fibrous sheaths around the issuing spinal nerves. The dural sheath of the optic nerve is connected at one end with the periosteum of the orbit, and at the other with the sclerotic. At the caudal end of the spinal cord the



dura mater forms a sheath around the filum terminale, and fuses at last with the periosteum of the sacrum.

A tessellated epithelium can be shown to cover the surfaces of both the parietal and visceral dura mater (fig. 206). To see the epithelium it is best to take the dura of a young animal just killed. The membrane is spread out in a watch-glass or shallow dish, and acted upon for several minutes by a 0·2 to 0·5 per cent. solution of nitrate of silver. The preparation is then thoroughly rinsed in distilled water and preserved in glycerin or, after dehydration, in dammar varnish.

After exposure to the light, the boundaries of the epithelial cells become evident. Small dark areas appear between them which must probably be regarded as stigmata. The substance of the dura is composed of coarse connective tissue, with only a few elastic fibres. Numbers of Waldeyer's plasma-cells (connective-tissue cells with abundant coarsely granular protoplasm) are said to be found in the dura mater in addition to the usual connective-tissue cells.

Without further preparation one can see with the naked eye that the large blood-vessels of the dura lie nearer to the parietal layer of the dura than to its visceral layer. If a very thin dura which has been obtained from a suitable animal is prepared as recommended above, it is seen that the relation to it of its vessels is peculiar (fig. 207).

The arteries first attract attention, the boundaries of their epithelial cells, as well as the cement substance between the muscle-fibres, being distinctly shown. In addition, outlines of epithelial cells are seen on either side of the artery; these cells line a straight space which adjoins the wall of the artery and sends out numerous irregular branches on either side. The side spaces are connected with one another into a characteristic network. Not rarely the branches cross the artery.

The meaning of these spaces is still in dispute. They are injected with more or less ease from the blood-vessels. Sometimes blood-corpuscles are seen in them; but, despite this, they are not to be regarded as genuine veins, but as peculiar appendages to the system of blood-vessels, for no blood normally circulates through them. If they were filled with blood, the dura of a living animal would appear of a dark violet colour, so close is the network. It may be accepted that they communicate with the subdural space by means of the stigmata on the visceral surface of the dura; and that on the other side they open into the real blood-vascular system.

*Langer* says the fine arteries of the dura mater pass over into veins of much greater calibre by means of funnels resting by their bases upon the veins and receiving the arteries into their apices.

The nerves of the dura are fairly numerous. Some of them form a moderately rich network in the substance of the dura itself, others are intended for its blood-vessels. Vater's corpuscles have been observed in the dura (*Krause*).



The following are the most important **pathological changes** in the dura mater :—

Not rarely, in old people especially, concentrically laminated glancing concretions, corpora arenacea (fig. 208), are found in the dura. They hardly exceed 80  $\mu$  in diameter, and are surrounded by a many-layered envelope of connective tissue. They consist of phosphate and carbonate of lime, and when in large numbers are easily detected on touching the visceral surface of the membrane. Their favourite situation is on the dura of the basis cerebri, and especially on the clivus. Concretions are also scattered about in many tumours of this membrane. When present in excessive quantity they constitute psammomata. The latter have usually an abundant coarse connective-tissue scaffolding which supports large numbers of round mulberry-shaped or elongated corpora arenacea. In many psammomata we meet with calcified trabeculae of connective tissue rather than free corpora arenacea, or (as *Cornil* and *Ranvier* have demonstrated) with concretions which have originated from calcifications or sinuosity in the vessels. In preparations coloured by Weigert's hæmatoxylin-method these calcifications stand out conspicuously black.

OSSIFICATION of the dura occurs under otherwise normal conditions; and in many animals it is in places always converted into bone. As instances of this may be quoted, the falx of the dolphin and to a less extent of the seal, probably also of the ornithorhynchus; the tentorium of certain carnivores, especially the cat and the bear, and to a smaller degree of such ungulates as the horse, pachyderms, etc. Bony neoplasms are more common in the dura of people suffering from cerebral disease, especially epilepsy, than in healthy brains; in women ossification is less common than in men. Ossification occurs most commonly in the falx cerebri or its immediate neighbourhood, where the bony plate may reach a diameter of 8 cm. It is more common on the left side of the falx than on the right.

Ossification of the spinal dura is extremely rare.

Warty thickening of the dura, which may involve the pia mater and the cortex, is a frequent result of syphilis.

TUMOURS OF THE DURA are either primary or metastatic. The primary forms belong, for the most part, to the group of tumours of the connective tissue, fibromata, fibro-sarcomata. The pure or fixed fibromata, and, above all, the endotheliomata of the dura have a tendency to take on a rounded alveolar form (tumour fibro-plasticus). Endothelial tumours, too, are frequently met with; lipomata are rare. Primary tuberculosis of the dura does not occur. Among secondary tumours the commonest are carcinomata of all kinds. As has already been mentioned, single corpora arenacea are found in many tumours of the dura. Where they occur in greater numbers the result is a transition form to the psammomata of which I have just spoken.

Inflammation of the dura mater is termed PACHYMENINGITIS.

Simple purulent pachymeningitis, in which the dura is found to be occupied by pus-corpuscles, is rare; such inflammation is usually traumatic or due to extension from other localities.



A chronic process, in which a false membrane (or new membrane) containing blood-pigment is deposited on the inner side of the dura, is more common. It is termed pachymeningitis interna hæmorrhagica (pigmentosa). The deposition on the inner side may amount to no more than the formation of a delicate, usually rust-coloured, spotted membrane, or may (owing to the deposition of many such membranes, one above the other) constitute a thick crust almost half a centimeter through.

The processes by which this deposition is effected are of two kinds, resulting in membranes of different structure.

It may happen that a small hæmorrhage is effused into the subdural space from the vessels of the dura mater, and that the fibrin of the effused blood, which usually is small in quantity, coagulating on its visceral side, the blood is encapsuled in a sac with the dura mater for its outer wall, and the coagulated fibrin for its inner wall, hæmatoma duræ matris. By-and-



Fig. 209.—Pseudo-membrane formed on the dura mater after a small hæmorrhage. A part of the latter is visible at the lower edge of the figure; scattered lymph-corpuses lying among the fibrin fibres. *Magn. 40.*



Fig. 210.—Neo-membrane of the dura mater resulting from pachymeningitis hæmorrhagica. *Magn. 40.*

bye the contents of the sac are absorbed, and a layer of fibrin coloured with blood-pigment is left as a false membrane (fig. 209).

The second, commoner, and more important variety of pachymeningitis interna runs quite a different course. At first a very delicate layer is formed on the inner side of the dura, as the result of a condition of irritation accompanied probably with emigration of leucocytes out of the dura. The lymphoid cells then begin to exhibit their formative activity, constructing a thin connective-tissue membrane, in which vessels of wide calibre, but thin walls, make their appearance. They do not at first contain blood (fig. 210). There is thus developed not a pseudo-membrane but an organised neo-membrane devoid at first of blood-corpuses, and not stained with blood-pigment. The vessels of the neo-membrane form communications with the vessels of the dura, and so obtain a supply of blood.



The connecting vessels also are very delicate; they easily rupture, and thus occur hæmorrhages between the dura and the neo-membrane. In turn the effused blood is absorbed, but some of its colouring-matter remains behind as the contents of what were once lymphoid cells. The pigment-containing cells are very common in the vicinity of the blood-vessels. Such neo-membranes may be deposited layer upon layer (so, too, may, perhaps, the pseudo-membranes of the other forms of pachymeningitis), and thus give rise to the already-mentioned thick covering. Concretions are frequently met with in these neo-membranes.

Large encapsuled hæmorrhages which are only partially absorbed constitute permanent hæmatomata.

The anatomical condition resulting from pachymeningitis interna is most often found in chronic cerebral disease, especially dementia paralytica and alcoholism. The first-mentioned form especially is commonest in advanced age; but it is sometimes observed in children under a year old. In these cases it is probably caused by injuries at birth. The dura mater spinalis is normally very thick on the ventral side of the cervical cord. An abnormal overgrowth of the dura also occurs in this situation, which may attain such dimensions as to cause pressure on the cord (*Joffroy*), pachymeningitis cervicalis hypertrophica.

Coarse, crust-like thickening of the dura, extending sometimes to the inner membranes and the cortex, is frequently observed in syphilis. A similar thickening of the dura spinalis results in compression-myelitis.

## B. ARACHNOIDEA (Meninx Serosa, Visceral Layer of the Arachnoid).

The arachnoidea does not follow the irregularities in the contour of the brain; on the contrary, it is adherent to the dura mater, both cerebral and spinal being separated from the pia by a considerable space bridged across by connecting threads or platelets (subarachnoid tissue).

Thus the arachnoid does not dip into the fissures, but retires in many places a considerable distance from the brain, leaving large spaces, the subarachnoid sinuses (*cisternæ subarachnoidales*). Of these, two deserve especial mention:—

(1) SINUS SUBARACHNOIDALIS POSTERIOR (*cisterna magna cerebello-medullaris*) between the back of the cerebellum and the medulla oblongata. Here the arachnoid spreads like a veil from the vermis superior and the posterior part of the dorsal cerebellar surface over the vallecule to the medulla oblongata below the *calamus scriptorius*.

(2) SINUS SUBARACHNOIDALIS BASALIS is shaped like a star with five rays. The body of the star is formed by the arachnoid sweeping forwards from the anterior border of the pons over the *corpora caudicantia*, the *infundibulum*, and the optic chiasm. The rays of the star are thus formed—the subarachnoid sinus extends around the *crura cerebri* on either side;



in front two paired lateral diverticula extend into the Sylvian fossæ, while the fifth ray is directed forwards and upwards into the space which commences in front of the chiasm, and is prolonged in the median fissure of the brain above the corpus callosum.

All the nerves which leave the skull-case receive a sheath from the arachnoid.

The arachnoid membrane of the cord retains its individuality throughout; it takes part in the formation of the sheath of the filum terminale as well as of the nerves. Numerous threads of subarachnoid tissue connect it with the spinalis, especially on its dorsal surface.

Certain peculiar excrescences of the arachnoid (which are most numerous in the neighbourhood of the great longitudinal fissure, but occur also on the side of the cerebellum, sometimes at the apex of the temporal lobe, and rarely in other places) are termed arachnoid plexuses [glandulæ Pacchioni]. They will be described in connection with the histology of the membrane.

The arachnoidea consists of connective-tissue fibres, and of the nuclei belonging to them. It contains neither vessels nor nerves. On either

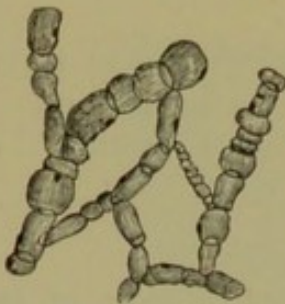


Fig. 211.—Trabeculae of the arachnoid membrane after treatment with acetic acid. *Magn.* 200.

side it is covered with an exceedingly delicate tessellated epithelium. The connective-tissue fibrillæ are not, as a rule, united into definite bundles, but either course quite irregularly or in two diametrically opposite directions (arachnoidea spinalis). The threads, after which the web-like membrane is named, spread out from the arachnoid like roots. They always consist of a central core or connective-tissue bundle invested with an epithelial sheath. For the rest, its structure, despite the closest examination by *Key* and *Retzius*, is hardly understood. When acted on by acetic acid, the threads exhibit circular or spiral constrictions (fig. 211), formerly attributed to

elastic fibres. The view to which observers now incline is that these constrictions are produced by a cellular investment of the bundle. Besides this, many bundles are surrounded with a broad homogeneous or faintly striated sheath, as to the meaning of which it is impossible at present to draw any conclusions.

To examine the structure of the arachnoid membrane it is well to take it from situations in which it is widely separated from the pia, as around the cauda equina or in the posterior subarachnoid sinus.

Subarachnoid tissue is best obtained from the sinus basalis. After treating the fibres for some time with acetic acid the preparation may be washed and mounted in glycerin.

The ARACHNOID PLEXUSES (Pacchionian granulations, corpuscles, or glands) are knobby, cauliflower-shaped, pedunculated excrescences of the arachnoid with which they agree in minute structure; they consist of loose connective tissue like that of the arachnoid covered with epithelium. Scat-



tered arenaceous corpuscles may be found in these plexuses as everywhere else over the arachnoid.

They grow out into the subdural space, but do not stop there; for they force their way into the substance of the dura where it offers least resistance or presents preformed cavities. Thus they press themselves into the sinuses as well as into the venous spaces, *Ps* (fig. 205), on either side of the superior longitudinal sinus.

The parasinoidal spaces (*lacunæ laterales*) are found at the spots where the great veins which come up from the surface of the hemispheres enter the dura. Through them the blood is discharged into the superior longitudinal sinus. Like the sinus, they are lined inside with epithelium. If the dura mater is stript off from the parasinoidal spaces, or even from the sinus, the floor of the spaces is seen to be lifted up by the Pacchionian granulations. The Pacchionian body does not make its way through the wall of the space, but pushes it in front of itself, and so comes to be invested by its epithelium (*G*). Sometimes, especially in the brains of old persons, we find depressions on the inner surface of the skull (*foveæ glandulares*), sometimes so deep that the bone is perforated. These excavations are probably due, less to the Pacchionian granulations themselves than to the diverticula of the veins.

Pigments injected into the subarachnoid space find their way into the meshes of the arachnoidal plexuses, and through its complicated epithelial coat into the parasinoidal spaces and the veins. In purulent and bloody effusions into the subarachnoid space, pus-corpuscles and blood-corpuscles are found in the Pacchionian bodies.

In children these bodies may be quite absent, and they are never much developed before the tenth year. They are found in many animals, especially the larger ones, but they are certainly not so well developed as in Man.

Of the **pathological changes** which affect the arachnoid, only the following will be mentioned:—

Small plates of bone without any essentially pathological significance are sometimes met with in the arachnoid, usually over the frontal lobe. They are more common in the arachnoidea spinalis, especially over the dorsal surface of the lumbar and lower dorsal cord. Here they are occasionally very large, measuring several centimeters in length. These little plates, as thin as paper, frequently occur in advanced age, in cases of chronic disease of the spinal cord, and in dementia paralytica. The external surface is fairly smooth, but that towards the subarachnoidal space is usually set with knotted and knobby excrescences.

Cartilaginous plates are also found, consisting of a firm homogeneous inter-cellular substance arranged in layers. Between the layers are cells (?) with oval nuclei and sclerosed threads of connective tissue, which are continued into the normal arachnoid threads. As the condition advances chalk-salts are deposited in the plates, and in some cases actual osteomata are formed, medullary cavities and cells, and even blood-vessels, originating from the dura mater (*Zanda*). Lamellæ and bone-corpuscles can occasionally be detected.



In the brains of many adults, almost all of advanced age, small, slightly opaque patches are to be seen here and there in the arachnoidea.

The arachnoid may become extensively thickened and opaque in consequence of chronic irritation, especially over the convexity of the great brain near the middle line, and over the large vessels of the pia. This condition is most often found in lunatics and drunkards, but even in simple atrophy (especially senile atrophy) opaque patches are observed.

Quite different to the above are certain small disseminated white patches of thickened arachnoidea, which may be scattered over the whole convexity after chronic brain-disease, in idiots more especially.

Numerous little overgrowths of the superficial endothelium are likewise found in cases of chronic disease of the brain, especially dementia paralytica. They give the arachnoidea a rough, gritty appearance.

Small accumulations of fat are not seldom found in the arachnoidal tissue at the base of the brain, particularly in the vicinity of the corpora caudantia. They sometimes grow so large as to form small lipomas.

### C. PIA MATER (*Meninx Vasculosa*, *Tunica Propria*).

The pia mater cerebialis, which closely invests the surface of the brain, not only sinks down into all the fissures of the cerebrum and cerebellum (fig. 205), but also enters by means of special slits into the interior of the ventricles, where it forms the *telæ choroideæ*. In a similar way the pia mater spinalis adheres to the spinal cord sending the triangular folds already mentioned, the *ligamentum denticulatum*, to the dura. The connections between pia and arachnoidea have been already described. The *filum terminale*, as well as all nerves coming out of the cerebro-spinal axis, receive sheaths from the pia mater.

The pia mater cerebialis is a somewhat delicate connective-tissue membrane rich in nuclei. In and under this membrane arteries and veins as well as capillaries, the latter relatively the least abundant, spread out before giving off their lateral branches, which descend vertically into the brain-substance. The vessels of the pia are surrounded by lymph-spaces, and carry sheaths from the pia with them into the substance of the brain. These lymph-spaces communicate directly with the adventitial spaces round the vessels in the brain, while the perivascular spaces, as well as, perhaps, other free lymph-channels—from the periganglionic lymph-spaces, it may be—would open into the still hypothetical epicerebral space. The epithelium which covers the arachnoid is continued on to the pia.

By the inner, non-vascular layer of the pia mater cerebialis, formerly regarded as distinct, was meant a delicate glial membrane, which can only be recognised where it covers the cerebellum as a basal membrane. It has nothing to do with the pia.

In the spinal cord the pia consists of two layers; both rather coarse. The external layer, composed for the most part of longitudinal fibres, supports the blood-vessels, which are disposed less closely than in the pia



cerebralis. The inner non-vascular layer is composed of strong circular connective fibres.

The whole of the pia enters into the sulcus longitudinalis ventralis, but only the inner layer enters the dorsal sulcus.

Numerous branched pigment-cells are often found in the pia, especially in old persons. They are most numerous on the ventral side of the medulla, which often appears, in consequence, of a smoky colour to the naked eye. These pigment-cells may be met with throughout the whole length of the spinal cord in the external layer of the pia mater; and not rarely in the internal layer also. On the other side, on the base of the brain the pigment-cells can be followed forwards as far as the olfactory bulb and the fossa Sylvii. There is no proof of a relation between the colour of the skin and hair and the pigment in the pia mater.

Within the pia mater is a rich web of sympathetic nerves, intended for the vessels it contains. Besides these nerves, we see in the pia mater spinalis, especially on its ventral surface, fine nerve-fibres which pass directly into the pia from the substance of the cord, course in it for a considerable distance, and end either in button-like swellings or in terminal bodies, which are said to resemble Meissner's touch-corpuscles (*Aronson*).

In many reptiles and amphibious animals, as well as in some mammals, such as the horse, dog, cat, seal (*Schlesinger*), a long fibrous band, oval in cross-section, is enveloped in the substance of the pia mater on the lateral surface of the cord. It exhibits the same histological structure as the dura mater, with which it is connected by means of the ligamentum denticulatum.

Amongst **pathological changes** in the pia, **HYPERÆMIA** and **HÆMORRHAGE** may be mentioned.

The condition in which the pia mater and cortex adhere firmly to one another (unite, in the common phrase), found, usually over the frontal lobe, in dementia paralytica, is not due, as has been sometimes stated, to a numerical increase of blood-vessels. The explanation lies (in part, at least) in the softening of the deeper layers, which renders the cortex apt to tear, while the submeningeal layer is thickened, and so seems more closely connected with the pia.

The same alterations in the contents of the **LYMPHATIC SHEATHS** of its blood-vessels are met with, as in the case of the sheaths of the intracerebral vessels.

Secondary **PURULENT MENINGITIS** (lepto-meningitis purulenta) is often observed. Different kinds of bacteria must be taken into consideration in studying the etiology of this disease. Of these the diplococci of pneumonia are the most important; they are found in from 60 to 70 per cent. of the cases under observation, and are said to occur even without declared pneumonia. The occurrence of pus is not limited, however, to the substance of the pia; it is found in the subarachnoid space, the



Fig. 212. — Pia mater in meningitis tuberculosa. *Magn.* 15.



epicerebral space, and also in the lymphatic sheaths around the cerebral vessels. Pus corpuscles also penetrate directly into the cortex, causing, apparently, degeneration of the tangential fibres.

TUBERCULOUS BASILAR MENINGITIS is characterised chiefly by the appearance of little elevations on the pia, varying from the smallest dimensions up to the size of a millet-seed. They consist of tubercle-cells, and are deposited by preference around the vessels on the base of the brain and in the Sylvian fossa (fig. 212). The cortex is almost always diseased too; it is usually hyperæmic under the affected parts of the pia, and large numbers of small hæmorrhages are present.

Many Tumours of the brain and spine originate in the pia mater.

Many (cancer of the plexus, for example) spread rankly in a thin layer over a large area, until—to take an instance—the whole medulla oblongata is enveloped in a cancerous substance hardly recognisable by the naked eye.

In old age, amyloid bodies belonging to the cortical gleia-stratum are sometimes found adhering to the pia mater; a circumstance which may be connected with many chronic diseases of the central nervous system.

An American waterfowl, *Plotinus aninga*, is said to invariably carry a large ball of thread-worms in the meninges, over the cerebellum, without being in the least the worse for it.

It is by no means unusual to find *cysticercus* vesicles in the inner meninges of the brain (of the cerebrum especially). They often occur in very large numbers. *Cysticercus racemosus*, which settles by preference in the basal subarachnoidal space, is an uncommon variety.

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We have already described the topographical disposition of the **telæ choroideæ** and the **plexus choroidei** of the ventricles of the cerebrum and cerebellum.

It will suffice to recall here the fact that these structures are reduplications involuted from the pia mater. The telæ choroideæ correspond exactly in structure with the pia mater. On the surface turned towards the ventricle are the remnants of the rudiment of the brain.

The histology of the plexus choroidei demands closer examination. In them the pia mater seems to be reduced to a nearly structureless membrane, in the substance of which no blood-vessels run. On the other hand, peculiar vessels, capillaries of wide calibre, are pushed forwards in the reduplication of the membrane so that they are enclosed by it on all sides. The numerous convolutions of these capillaries during their long course give to the plexus its characteristic knotted appearance. The plexus is covered on its ventricular surface by a single layer of epithelial cells of a peculiar kind (fig. 213). Although of various shapes these cells incline to a cubical form. Their edges and corners are drawn out into processes, by means of which they dovetail with one another. A round nucleus lies in a coarsely granular protoplasm, but almost every cell contains, in addition to the nucleus, a highly refractive, bright, yellow, or yellowish-brown body. As



this body is coloured dark on the addition of osmic acid, it may be looked upon as probably formed of some substance related to fat. Sometimes it assumes a rod-like or ring-like form. The structure of the choroidal plexus is in a high degree suggestive of an evolved gland. [It recalls to mind the glomerular plexus of a renal tubule.] It conveys the impression that the cells of the neuro-epithelium, instead of forming nerve-substance, have been transformed, as it were, into glandular cells concerned with the secretion of the liquor cerebro-spinalis. We are the more entitled to take this view, because the cerebro-spinal fluid cannot by any means be regarded as a simple serous exudation; its chemical constitution shows that it is a specific fluid. It contains but few formed elements.



Fig. 213. — Epithelium of the choroid plexus. *Magn.* 200.

Among the accessory bodies found in the choroidal plexus may be mentioned fat-granules, brown pigment, and especially chalky concretions of smaller or larger size. No pathological significance can be attributed to these substances, nor to the frequent calcification of vessels in the choroidal plexus. Tumours, such as lipomas, may affect the choroidal plexus. Primary actinomyces was observed by *Bollinger*. Cysts with contents more or less fluid are hardly ever absent in old people; they may, however, be found at birth. Their favourite location is the glomus of the plexus lateralis. *Schnopfhagen's* view that they are formed by the dropsical separation from one another of the two layers of the pia which constitute the tela and plexus is most probably correct.

In the horse, concretions of inorganic material (carbonate or phosphate of lime) or of cholesterin are constantly met with (*Faivre*); they may be very numerous and even as large as hen's eggs.

#### D. THE GREAT VESSELS OF THE BRAIN.

Within the skull-case arteries and veins do not run in company as they do in other organs. Leaving out of consideration the great venous sinuses of the dura mater, we may say that all the larger arteries are found on the base of the brain, while the larger veins are directed towards its convexity.

The method in which the vessels within the brain divide is well known, thanks to the investigations of *Heubner* and *Duret*; here, however, the subject can only be treated in outline.

The brain is supplied with blood by two arteries on each side, the internal carotid and the vertebral.

The internal carotid artery, *Ci* (fig. 214), advances along the side of the tuber olfactorium, and divides, after it has given off the ophthalmic artery which courses forwards, into its two chief branches, the anterior and middle cerebral arteries.

Arteria cerebri anterior, *Ca* (arteria corporis callosi), winds at first



towards the middle line, slips over the optic nerves, and then bends round into the great longitudinal fissure, where it can be followed a long way backwards on the upper surface of the corpus callosum.

At the spot where the anterior cerebral arteries of the two sides assume a sagittal direction, they are placed so close together that a very short connecting branch, *Coa* (arteria communicans anterior), suffices for their anastomosis. At the place where the artery slings itself round the corpus callosum it gives off a fine branch for the dura mater, which courses backwards, along the lower edge of the falx (*Langer*).

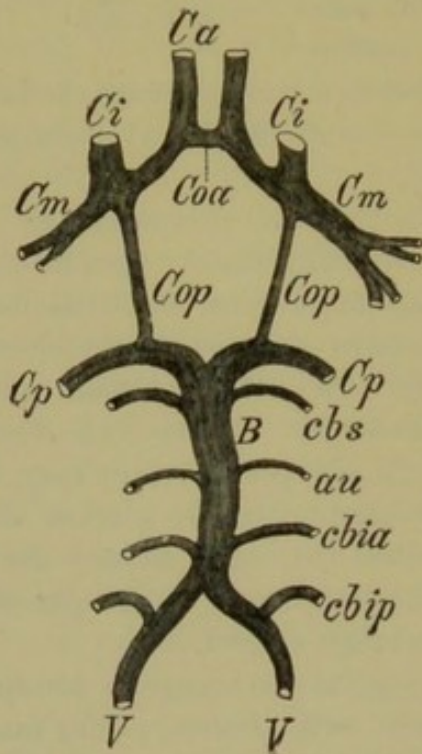


Fig. 214.—Arteries at the base of the brain; circle of Willis.—*Ci*, a. carotis interna; *Ca*, a. cerebri anterior; *Cm*, a. cerebri media; *Cp*, a. cerebri posterior; *Coa*, a. communicans anterior; *Cop*, a. communicans posterior; *V*, a. vertebralis; *B*, a. basilaris; *cbs*, a. cerebelli superior; *cbia*, a. cerebelli inferior anterior; *cbip*, a. cerebelli inferior posterior; *au*, a. auditiva.

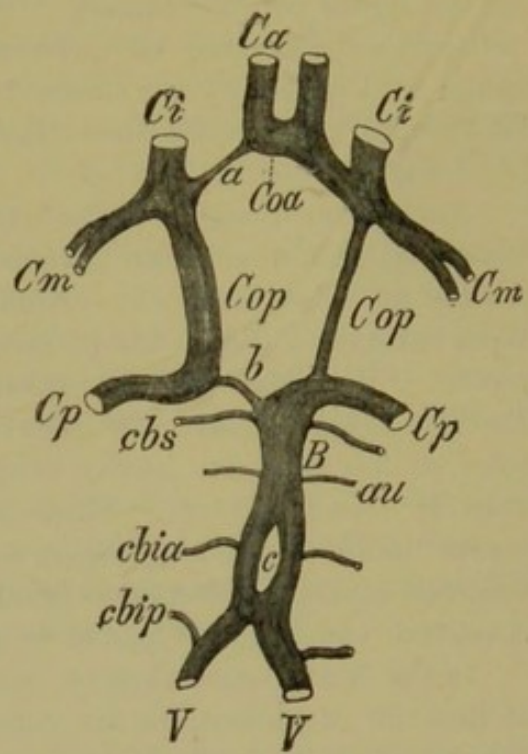


Fig. 215.—Anomalies of the circle of Willis. Lettering as in fig. 214.—*a*, a. cerebri anterior; *b*, a. cerebri posterior, reduced to the dimensions of communicating arteries; *c*, island in the vertebral artery.

The arteria cerebri media, *Cm* (arteria fossæ Sylvii seu transversa cerebri), must be looked upon as the direct continuation of the internal carotid. Hence it is that emboli which have come up the latter vessel are more likely to continue their course into the middle than into the anterior cerebral artery. It turns sideways so as to enter the fossa Sylvii, where it soon divides into a varying number of branches.

Each of the two vertebral arteries (*V*) gives off an arteria cerebelli inferior posterior (*cbip*), and then unites with its fellow at the back of the pons into a single trunk, the basilar artery (*B*). The basilar artery passes forwards in the median line with, usually, a slight convexity to the left,



and, as a rule, gives off at right angles three small arteries from either side; arteria cerebelli inferior anterior (*cbia*), arteria auditiva (*au*), and arteria cerebelli superior (*cbs*). At the proximal border of the pons the basilar artery again divides into two branches directed straight outwards, arteriæ cerebri posteriores, *Cp* (arteriæ profundæ cerebri).

Immediately before the internal carotid passes over into the middle cerebral, or just from the commencement of the latter, come off two branches, arteria communicans posterior, *Cop*, and the arteria choroidea anterior. The former is usually a rather narrow vessel which passes backwards towards the posterior cerebral, which it joins at a distance of scarcely as much as 1 mm. from the point where the arteria basilaris bifurcates. In this way there is formed on the base of the brain a hexagonal or heptagonal ring, *circulus arteriosus Willisii* (hexagon, polygon of Willis).

After giving off the posterior communicating artery, the internal carotid, or, as it is here called, the middle cerebral, gives off backwards a second fine branch, arteria choroidea. This artery courses along the tractus opticus, by which it is conducted into the plexus choroideus of the descending horn of the lateral ventricle.

From these large vessels the arteries for the brain substance come off in a two-fold way. So long as the chief arteries lie on the base of the brain they give off fine branches for the brain-substance, which, as they do not anastomose with one another, belong to the class of vessels termed 'end arteries' (Heubner's basilar area). Over the whole of the rest of the surface of the brain the larger arteries gradually break up dichotomously (Heubner's cortical area). Neighbouring vascular territories are in connection with one another by means of numerous anastomoses in the pia mater. Anastomoses between the vessels of the cortical areas of the two hemispheres are very uncommon.

The direction of the fissures on the surface of the brain is almost entirely unconnected with the course of the vessels. The central parts of the brain, including the central ganglia and a great portion of the white substance which adjoins them, are exclusively supplied from the basal system; the cortex and the medullary substance beneath it are nourished from the vessels of the cortical system.

The whole surface of each hemisphere may be divided up into three areas corresponding to the three chief arteries of the great brain:—

(1) Area of the arteria cerebri anterior, which includes (on the convex surface of the brain) the whole of the upper and a small part of the middle frontal convolutions, the upper third of both central convolutions, and the larger part of the upper parietal lobe; the whole of the anterior and middle parts of the mesial surface, to beyond the middle of the præcuneus. The mesial portion of the orbital surface (inclusive of the trigonum olfactorium and olfactory tract) is supplied, often throughout, and always to some extent, by a constant branch, the arteria olfactoria.

(2) Area of the arteria cerebri media. This is restricted to the convex surface of the hemisphere, where it includes those parts of the frontal and parietal lobes not supplied by the arteria superior anterior, as well



as the anterior portion of the occipital lobe, and, perhaps, the two upper convolutions of the temporal lobe: and on the orbital surface the variable area which is not supplied by the *arteria cerebri anterior*. On the median surface it supplies at the utmost a small branch in the neighbourhood of the uncus (*arteria gyri uncinati*).

The number of branches into which this artery divides in the Sylvian fossa varies from four to ten. Five main branches can usually be more or less clearly distinguished; they are named after the areas in which they principally circulate. From before backward, they are: *arteria gyri frontalis inferioris*, *arteria gyri centralis anterioris*, *arteria gyri centralis posterioris*, *arteria lobuli parietalis inferioris*, *arteria lobi temporalis*. The

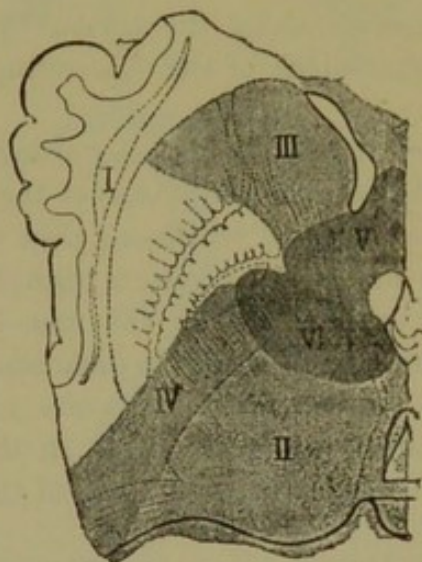


Fig. 216.—Horizontal section through the great brain, showing the region occupied by the several cerebral arteries (after Kolisko and Radlich).—I, region of the *a. cerebri media*; II, of the *a. c. posterior*; III, of the *a. c. anterior*; IV, of the *a. choroidea anterior*; V, of the carotid; VI, of the *a. communicans posterior*.

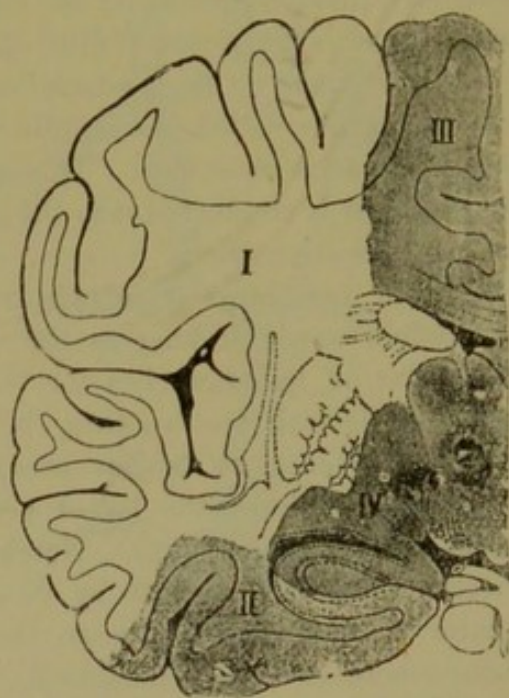


Fig. 217.—Frontal section through the great brain (after Kolisko and Radlich).

convolutions of the island of Reil are supplied by small side-branches of the larger vessels.

(3) Area of the *arteria cerebri posterior*, the posterior part of the occipital lobe on the convex side of the brain, and the whole of it on the mesial side, together with the adjoining portion of the præcuneus, and as much of the temporal lobe as is not occupied by the *arteria cerebri media*.

The behaviour of the central arteries—those, that is, which course within the brain—is exceptionally interesting, as it may be of great importance pathologically (in hæmorrhages and embolisms; see figs. 216 and 217).

They are usually rather fine, and go off at right angles to the large



trunks,—the carotid (V), the arteria cerebri anterior (III), the arteria choroidea anterior (IV), the arteria cerebri media (I), the arteria communicans posterior (VI), and the arteria cerebri posterior (II).

*Kolisko* has drawn attention to the peculiarities in behaviour of the central arteries which originate from the arteria cerebri anterior. These can be divided into long and short arteries. The former take rise in close proximity to the arteria communicans anterior (one or two on either side) and course straight back to the lamina perforata anterior, a disposition which greatly favours the occurrence of coagulations and derangements of the circulation. Consequently, the area supplied by it (the head of the nucleus caudatus, part of the anterior limb of the inner capsule, and of the anterior portion of the nucleus lenticularis) is peculiarly liable to softening. The short arteries are remarkable for their extreme fineness, which likewise conduces greatly to the inception of softening in the area supplied by them (anterior part of both segments of the nucleus lenticularis and the adjoining part of the internal capsule).

The central arteries which go off from the arteria cerebri media supply, at least in part, the three great ganglia and the internal capsule. The fine branches which rise from the anterior and median cerebral arteries and supply the nuclei caudatus and lenticularis were called by *Duret* 'artères lenticulo-striées'; those from the median cerebral artery which feed the nucleus lenticularis and optic thalamus he named 'artères lenticulo-optiques.'

From *Kolisko's* investigations the arrangement of the vessels for the internal capsule appears to be as follows:—

The upper divisions, all but the hindmost part (fig. 217, I), are supplied entirely by the arteria cerebri media; but in the deeper parts the anterior limb of the internal capsule is nourished chiefly by the anterior cerebral artery (fig. 216, III) and the carotid (V), and the posterior limb by the arteria communicans posterior and the arteria choroidea anterior (IV). The arteria choroidea anterior supplies the whole of the posterior part of the internal capsule, but only the deeper divisions of the anterior portion. In many brains the region of the knee of the capsule receives its blood-supply from a fine branch of the arteria communicans posterior (VI), named by *Kolisko* *Duret's* artery, which, in that case, supplies the anterior part of the optic thalamus as well. When the communicans posterior is very feebly developed this last-named region is also fed from the arteria choroidea anterior.

Since the most important motor and sensory tracts of the brain pass through the posterior limb of the internal capsule, it is easily understood that any derangement of the circulation in the region of the arteria choroidea anterior must be attended with very grave symptoms. If these manifest themselves chiefly in the motor functions, leaving the sensory perhaps unaffected, the explanation lies in the fact that the sensory region of the internal capsule often obtains a collateral supply by anastomoses with the arteria choroidea media and posterior (*Kolisko*).

The arteria choroidea media takes rise from the posterior cerebral



artery; the arteria choroidea posterior, which runs into the tela choroidea superior beside the vena Galeni, from the superior cerebral artery.

It should be particularly noted that, except for the circulus Willisii, the two hemispheres are almost independent as regards blood-supply. No large vessels cross the middle line. Sometimes, indeed, in the corpus callosum the capillary network of an arteriole can be seen to extend some way on the other side.

To what has already been said concerning the blood-supply of the cerebellum, I may add that the three cerebellar arteries vary greatly in size. The arteria cerebelli posterior, with its branches, spreads chiefly over the under surface of the cerebellum; the arteria cerebelli media over the upper surface; and the arteria cerebelli anterior over the vermis. Each arterial network, however, anastomoses frequently with the rest, and, apparently, with those of the other side. The arteria cerebelli media gives off a great branch to the corpus dentatum. Most of the extensive hæmorrhages into the cerebellum are caused by the bursting of this artery.

Proceeding from the region of the crus, through the pons, to the spinal end of the medulla oblongata, special attention is due to the arteries which run into the middle line on the ventral side and course dorsalwards in or alongside the raphe (*arteriæ centrales*). The two halves of the body appear to be nearly independent as far as these arteries are concerned, and anastomoses across the middle line are scarcely ever met with. It has also been demonstrated that in this part it is possible to inject a mesial region which has no connection whatever with the lateral portions (*Shimamura*).

The *venæ cerebrales superiores* are a succession of (in most cases) from ten to twelve veins, which pass upwards across the hemisphere and debouch into the sinus longitudinalis by the *lacunæ venosæ* (*cf. p. 476*). Before entering the sinus each is usually joined by a smaller vein which courses upwards on the median surface of the hemisphere. The largest *venæ cerebrales superiores* are found near the central convolutions and the temporal lobe.

A large constant vein (*vena Sylvii superficialis*) courses forwards on the surface, along the line of the Sylvian fissure. A fairly constant anastomosing branch ascends from this vein (*vena magna anastomotica*) and courses to the sinus longitudinalis, usually passing behind the central convolutions. The *vena Sylvii* and this branch are sometimes together called the *vena Trolardi*. Another thick and fairly constant branch courses downwards from the *vena Sylvii superficialis* and crosses the temporal lobe obliquely to reach the sinus lateralis.

The veins of the various internal parts of the brain collect into the *vena cerebri interna communis* (*vena magna Galeni*). It is about 1 cm. long and is formed chiefly by the confluence of the two *venæ cerebri internæ*, which collect the venous blood from the central parts of the cerebrum and run first in the plexus choroidei laterales, and then in the tela choroidea media.

The *vena cerebri interna communis* comes out through the great



transverse fissure, and discharges its contents into the sinus perpendicularis. Its upper side is generally marked by a concavity, in which the splenium corporis callosi rests.

The brain more than any other organ stands in need of a sufficient supply of blood. The united cross-section of the four arteries which supply it, however, bears a by no means constant relation to the size of the brain; on the contrary, it varies within wide limits (*Löwenfeld*).

[Not only does the brain require a large supply of blood, but the amount supplied to the organ as a whole (and still more the amount distributed to its several parts) must be capable of rapid and extensive fluctuations. Nervous tissues, in a more conspicuous degree than others, are in immediate relation to lymphatic spaces. Every nerve-cell lies in a little bath of lymph,\* while the whole cerebro-spinal axis is suspended in a sea of the same fluid, from which it extracts its nutrients, and into which it discharges its waste products; whilst the balancing of the spinal cord in the centre of the vertebral canal, by means of the ligamentum denticulatum, and the support of the brain upon the sinus subarachnoidalis basalis, protects the cerebro-spinal axis from sudden jars. The enclosure of the brain within the skull places the circulation under certain difficulties, but the abundant lymph serves to carry off any excess of pressure due to vascular turgescence. The venous sinuses, unlike veins in other parts of the body, are incapable of distension. The communications between the intra-cranial sinuses and the veins outside the skull, established by the emissary veins of Santorini (which traverse the frontal, parietal, mastoid, posterior condyloid, and other foramina), serve to keep down the pressure in the sinuses. Doubtless the rearrangement of the central grey matter, which occurs where the medulla oblongata replaces the spinal cord, is due to the need for distributing to the general lymph the pressure produced by local turgescence of the very important centres in this part of the axis, instead of allowing an active centre injuriously to compress its neighbours. The membranous roofs of the fourth and third ventricle confine the lymph less closely than would solid nerve-tissue. It has been suggested that the veins, which fill up the spaces between the great arteries that enter the base of the skull and the margins of the holes through which they pass, may serve as a self-regulating apparatus for the supply of blood to the brain, the veins, when distended, pressing upon, and so diminishing the calibre of the arteries; but the difference in pressure between the arterial and venous blood, in favour of the former, seems to make this impossible.

The experiments of *Corin* show that the pressure in the several arteries which supply the brain is very uniform. Even when three out of the four great affluents of the circle of Willis were tied, the pressure in the circle was unaffected.]

\* The cerebro-spinal fluid is functionally equivalent to lymph.



In most animals the part played by the carotid and vertebral arteries respectively in supplying the brain with blood is different to what it is in Man.

As compared with the carotids the vertebrals in most rodents and some other animals are very much the more strongly developed. On the other hand, in ruminants (as well as in the pig, and, probably, in the leopard) the vertebral arteries do not directly reach the brain. In these animals both carotids form a rete mirabile on the base of the skull outside the dura mater; not till it has passed this plexus does the carotid reach the base of the brain and unite with the basilar to form the circulus Willisii. The basilar artery is continued backwards on the ventral surface of the spinal cord as the *arteria spinalis anterior*. The two vertebral arteries remain all the time outside the dura mater, and only anastomose with the rete mirabile.

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The above-described typical arrangement of the great arteries on the base of the brain is subject to frequent variations of greater or less physiological importance.

We will mention the commoner **variations in the circle of Willis**. There may be several anterior communicating arteries; or, on the other hand, this artery may be altogether wanting, the anterior cerebrals growing together after an independent course of some distance.

The name of *arteria corporis callosi media* is given to an unpaired mesial branch which often takes rise from the anterior communicating artery and passes over the corpus callosum. It is constant in some apes.

Sometimes both anterior cerebral arteries are almost entirely derived from the same carotid artery (fig. 215). In this case there is, as a rule, a small branch of communication with the other side, connecting the anterior cerebral artery which comes from the opposite carotid with the carotid of its own side (*a*). In the same way it may happen that the posterior cerebral artery does not come off from the basilar, but from the carotid of the same side; being only connected with the anterior end of the basilar artery by an inconspicuous anastomosis (*b*). In this case the posterior communicating artery must be very strongly developed. The posterior communicating artery may, on the contrary, be wanting on one side.

Sometimes a fairly large vessel takes rise from the carotid within the sinus cavernosus and turns backwards towards the basilar artery. This has been repeatedly observed, and always in conjunction with abnormal weakness of the vertebral system.

Very often the origin of the basilar artery from the junction of the two vertebrals is indicated by the presence of a longitudinal septum in its interior; indeed the artery may be doubled for a certain distance, forming an 'island' (*c*). Very often the two vertebral arteries are not equally strong; usually it is the right which is the thinner.

In cases in which the abnormality marked *b* in fig. 215 occurs, the *arteria vertebralis* on the same side is apt to be extremely weak. This is



due to the fact that the arteria basilaris originates from the blending of the two vertebral arteries. The vertebral artery may also bend round almost completely into the arteria cerebelli inferior, its connection with the basilar artery being maintained only by a thin branch.

The vessels of the brain differ in no respects from those of other organs in their **minute structure**; the veins of the brain are devoid of valves.

Only the most important **diseases of the large vessels** of the brain will be mentioned.

EMBOLISM is frequent. In three-fourths of the cases it is the arteria fossæ Sylvii which is affected. Left and right equally often.

AUTOCHTHONOUS THROMBOSIS of the arteries of the brain must be distinguished from embolism.

Thrombosis of the sinuses is not rare. ANEURYSMAL ENLARGEMENT of the basal vessels is relatively uncommon. According to tables drawn up by *Lebert*, out of 86 cases of aneurysms of the vessels of the brain the basilar artery was affected 31 times, the middle cerebral 21. The remaining cases were divided amongst other arteries. The left side is more frequently affected than the right.

A high degree of distension of the basal arteries may follow upon a process of ENDARTERITIS, giving the whole circulus Willisii, and especially the arteria basilaris (which is 1.5 cm. in diameter) a swollen and mis-shapen look.

ATHEROMATOUS DEGENERATION is almost always met with in the vessels of the brains of old people. Sometimes it is difficult to distinguish an atheromatous degeneration from SYPHILITIC DISEASE. The latter disease is due to the growth of granulations or infiltrations, originating, probably, in the capillaries which supply the muscular coat of the vessel (*vasa vasorum*). The infiltration is spread out in the intima, and especially between the epithelium and the membrana fenestrata. Often in such cases of syphilitic disease a many-layered fenestrated membrane is seen, indicated in cross-section by a number of clear, highly refracting, waving lines. *Heubner* thinks that this is a new formation; but it is possible that it is due to splitting of the fenestrated membrane by the intercalation of granulations (*Rumpf*).

Syphilitic disease is distinguished from atheromatous disease by its greater tendency to active overgrowth and extension (even leading to thrombosis of the artery); while atheroma soon ends in a retrogressive process leading to calcification and fatty degeneration.

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## APPENDIX.

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### ROTATION OF THE GREAT BRAIN.

IN the spring of 1885 the *translator* propounded, as part of a general scheme of the structure of the central nervous system, the theory that the mammalian brain during its growth rotates upon itself.\* The rotation produces a loop or kink, giving to the whole brain somewhat the form of a ram's horn, and bringing the part which was at first in front, on to the under side of the back. At its first formation the cerebral hemisphere of the mammalian brain is directed, like that of the reptile, straight forwards; the foramen of Monro opens into the back of its ventricle, the anterior end of the hemisphere bears the olfactory bulb. In the adult condition the foramen of Monro opens into the front of the ventricle, the olfactory apparatus is attached through the pyriform lobe (*gyrus uncinatus*) to the inner side of the temporo-sphenoidal lobe.

This view as to the alteration in position of the great brain was the almost necessary deduction from certain conclusions as to the connections of the olfactory tract with the anterior end of the optic thalamus, *viâ* the fimbria, fornix, descending pillar of the fornix, corpus mammillare, and bundle of Vicq d'Azyr.

There are many reasons for believing that the olfactory nerve is connected in this way with the anterior end of the optic thalamus, and the circuitous route just sketched out is by no means difficult to follow. Its path is easily broken off from a hardened brain, of which it seems to form an organically distinct part, as shown in the accompanying sketch; and apart from the question of the arrangement in adult anatomy, we have, as will be shown presently, a certain amount of embryological evidence in favour of this extensive displacement of the olfactory tract. The formulation of such a path for the fibres of the olfactory tract almost necessarily presupposes a rotation of the brain; but it is not this connection only which the theory renders intelligible. Many other features in the plan of formation of the great brain are accounted for by this supposition of its rotation.

Among EXTERNAL APPEARANCES, the most suggestive is the progressive

\* *The Plan of the Central Nervous System.* Cambridge: Deighton, Bell & Co., 1885.



closing in of the fossa of Sylvius. The fissure of Sylvius, as has been shown (p. 99), is not, for the greater part of its extent, in any way comparable with the other fissures of the brain, since, instead of being formed like them, as a narrow slit-like depression on the smooth rounded surface, it makes its appearance before any other fissure, if we except the so-called rhinal fissure, as a dimpling of the mid part of the outer surface which gradually deepens into an extensive shallow fossa. The appearance of this fossa is due, apparently, to the traction exercised upon a part which will subsequently become the temporo-sphenoidal lobe by its attachment through the olfactory tract and bulb, to the cribriform plate of the ethmoid. As the great brain swells, a pitting of the outer surface is the necessary result of the attachment of its olfactory part to the skull. The fossa of Sylvius is subsequently converted into the fissure of Sylvius, a Y-shaped fissure, with a common portion dividing into an anterior and a posterior limb, by the

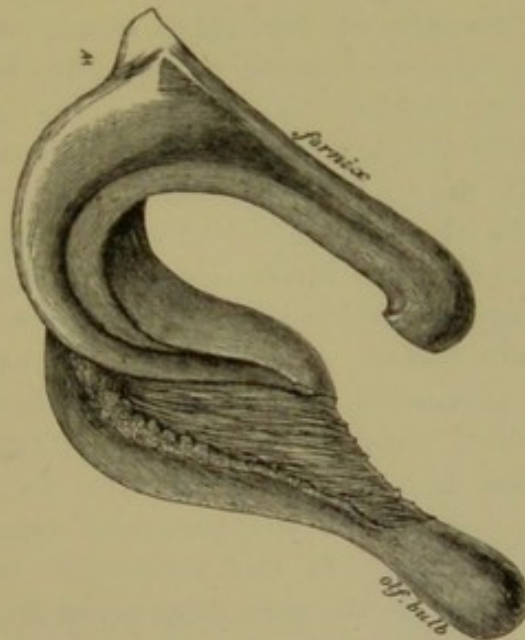


Fig. 218.—Fornix, pyriform lobe and olfactory bulb, broken off from the hardened brain of the Ox.

outgrowth in three swellings of the surface of the brain which borders it ; the operculum coming down between the limbs of the Y, the frontal and temporo-sphenoidal lobes closing up beneath the operculum. The want of homology between the fissure of Sylvius and other fissures is shown by its enclosing a considerable cortical area, the island of Reil, which originally formed the floor of the fossa. The fan-like arrangement of the fissures of the island of Reil indicates plainly enough the direction in which traction was exerted.

When viewing the outer surface of any mammalian brain, it is easy to convince oneself that it has undergone a rotation, and that the position of its parts has been altered from the form maintained amongst fishes, amphibia, and reptiles (for special reasons it is better to exclude from the comparison the bird's brain) in such a way that the temporo-sphenoidal lobe of the mammal's cerebrum corresponds to the anterior end of the brain of lower vertebrates.



Following closely upon the external form, the delimitation of the cortex into areas associated with peripheral nerves, presents itself as a test by which to try the theory. Recently, chiefly as the result of ablation experiments, the function of almost every part of the cortex has been determined, and although we are as yet far from possessing an accurate distributional map, we can nevertheless speak with assurance as to the general partition of work among its several territories. Undoubtedly the anterior end of the brain, particularly the Rolandic area, is in connection through the mediation of the grey matter of the spinal cord with the body nerves. The localities in which sensations are received through the 8th and 5th nerves, lie somewhere in the neighbourhood of the fissure of Sylvius; the 2nd nerve has its area of cortical distribution in the occipital lobe—the 1st nerve on the inner side of the temporo-sphenoidal lobe. Better, even, than direct experiment, the observation of brains of animals remarkable either for preponderance or for deficiency of particular senses, will help us to map out the cortex into functional areas (see p. 336, figs. 165, 166, 167). Whatever method be adopted for obtaining the necessary data, any sketch of the brain in which functional distribution is indicated, shows clearly enough that the order from before backwards in which the areas connected with the several nerves are situate, is in its largest features the reverse of that which obtains among the nerves themselves. In considering the bearing upon the question of the territorial allocation of the brain surface, it is important to have in one's mind a clear picture of the process of histogenetic differentiation of the nervous system. The cells from which nerve processes (fibres) extend into the cortex lie in the central grey tube. As yet we have no means of telling how they are guided to the particular areas in the cortex in which they are distributed. Is the connection between those areas and the primary centres in the cord determined from the first involution of the neuro-epithelial tube, or is such a connection established in a way which, for want of knowledge of the laws by which it is governed, may for the time be called 'by chance'? When the processes from a certain group of cells in the central grey tube take possession of a particular area of the cortex, are they guided to this area merely by its situation in relation to the skull-case or head, or owing to its primitive relation to the axis of the brain? Does the differentiation of the motor cells in the cortex precede the reception in this tissue of the sensory cell-processes, or does it depend upon their reception and the need thus established for a descending limb of the reflex arc? Many similar problems present themselves to warn us that we must not lay too much stress upon the allocation of the cortex to specific functions until we are far better equipped than at present with genetic data. It is sufficient for our purpose to consider only the larger groups of cortical centres. The arrangement of their sub-centres, as determined, for instance, in the marginal gyrus by Horsley and Schäfer, may for the present be regarded as a later allocation.



The body nerves have their cortical areas in front, and are followed by the nerves of the head; of these latter the optic nerve is indirectly connected with the back part of the upper surface, while the olfactory has its area in what we take to be the reflected portion. It seems as if the rotation or kinking over from before backwards were accompanied by a certain displacement from above downwards and outwards.

Passing now to the INTERNAL STRUCTURE of the hemisphere, so far as the course of fibres within its white substance is sufficiently well known to help us, we find further evidence of rotation. Leaving out of consideration all doubtful tracts, we have the classical observations of *Gratiolet*, which have been frequently confirmed, to show that the anterior end of the optic thalamus is connected through its inferior peduncle with the temporal lobe, the posterior end of the thalamus through the 'optic radiations' with the occipital lobe. Numberless

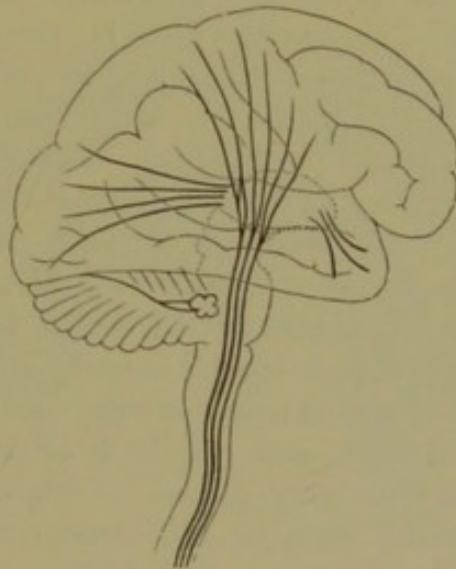


Fig. 219.—Diagram showing the tracts of fibres which connect the central grey tube with the cortex. The front of the thalamus is connected with the temporal lobe, the back of the thalamus with the occipital lobe, and the spinal cord with the Rolandic area.

recent observations have placed the connection of the grey matter of the spinal cord with the frontal and parietal lobes by means of the pyramidal tracts which occupy the anterior part of the internal capsule, beyond doubt. These three sets of fibres (1) of the internal capsule, (2) optic radiations, and (3) inferior peduncle, obviously cross one another, as shown in the accompanying diagram (fig. 219), plainly indicating that the cortex of the cerebrum and the grey matter of the basal part of the system extend in contrary directions. The force with which the crossing of these three sets of fibres appeals to the *translator*, will become apparent if his view as to the fundamental plan of construction of the central nervous system is borne in mind. The system arises as an involuted tube of epiblast. Throughout the spinal region the inner wall of the tube becomes grey matter; the outer wall constitutes the white columns of fibres. In the cephalic region a second layer



of grey matter, the cortex, is added on the outer side of the tube; all the grey matter of the system grows from one or other of these two grey layers. In the spinal cord, which only contains the tube of grey matter which borders the central canal, are situate all the primary centres of the body nerves; the grey matter contains the nerve-cells and plexus for the origin of motor and the reception of sensory fibres belonging to each metamer. Travelling up into the brain, no break in the continuity of the grey matter is to be observed. It lies in the floor of the fourth ventricle, around the aqueduct, and in the sides and floor of the third ventricle. No one doubts the continuity of plan as far as the anterior end of the iter; but hitherto it has not been recognised that the grey matter bordering the third ventricle is in functional continuity with the grey matter of the cord. The optic thalami are treated of as 'basal ganglia.' The olfactory and optic nerves are deprived of primary centres such as are accorded to all other sensory nerves. The modifications in structure of the central system, due to the situation peripherally in the olfactory bulb and retina of some of the grey matter, have been already pointed out (p. 328). The differences in structure between the thalamus and the rest of the central grey matter do not indicate a want of homology, but a partial homology, the homology of the thalamus with the sensory constituents of grey matter of the spinal cord *minus* those elements which in the case of the first two nerves are extra-axial, in the bulb and retina. If the optic thalamus is part of the anterior end of the central grey tube, the attachment of the extreme anterior end of the thalamus with the temporo-sphenoidal lobe, and the back of the thalamus with the occipital lobe, and of the grey matter of the spinal cord with the front of the hemisphere, supplies the strongest possible evidence of rotation.

Passing now to the consideration of one of the chief inter-cerebral tracts, we find in the arrangement of the fibres of the anterior commissure evidence of rotation of a most convincing kind. Fig. 220, which is a copy of the picture on page 490 of Schwalbe's *Neurologie*, accurately represents the peculiar twisting which the anterior commissure has undergone. It looks as if the middle of the commissure had been fixed, while its ends were twisted in such a way that the fibres which cross the median line on its under side, pass round in front to reach the upper side at its extremities; just such a torsion as would be produced by the rotation of the hemisphere round an axis situate just below and in front of the foramen of Monro.

In addition to the demonstration which the twisting of the anterior commissure affords of the fact of rotation, peculiar interest attaches to it, since it enables us to fix approximately the time at which rotation takes place. It must occur after this commissure is formed. There can be no doubt that the anterior commissure appears very early in the mammalian brain, for although we have no exact observations as to the time of its appearance in the individual, this conclusion may be drawn from its great



prominence in the lower forms of vertebrates. It is *par excellence* the commissure of birds and reptiles. The existence of a rudimentary corpus callosum in birds was assumed by *Meckel*, but the view of *Stieda*, that no such structure exists, is endorsed by most observers, *Rabl-Rukhard* and *Bellonci inter al.* On the other hand, *Stieda* recognises the existence of a corpus callosum in reptiles, but denies it in amphibia, where *Leuret*,

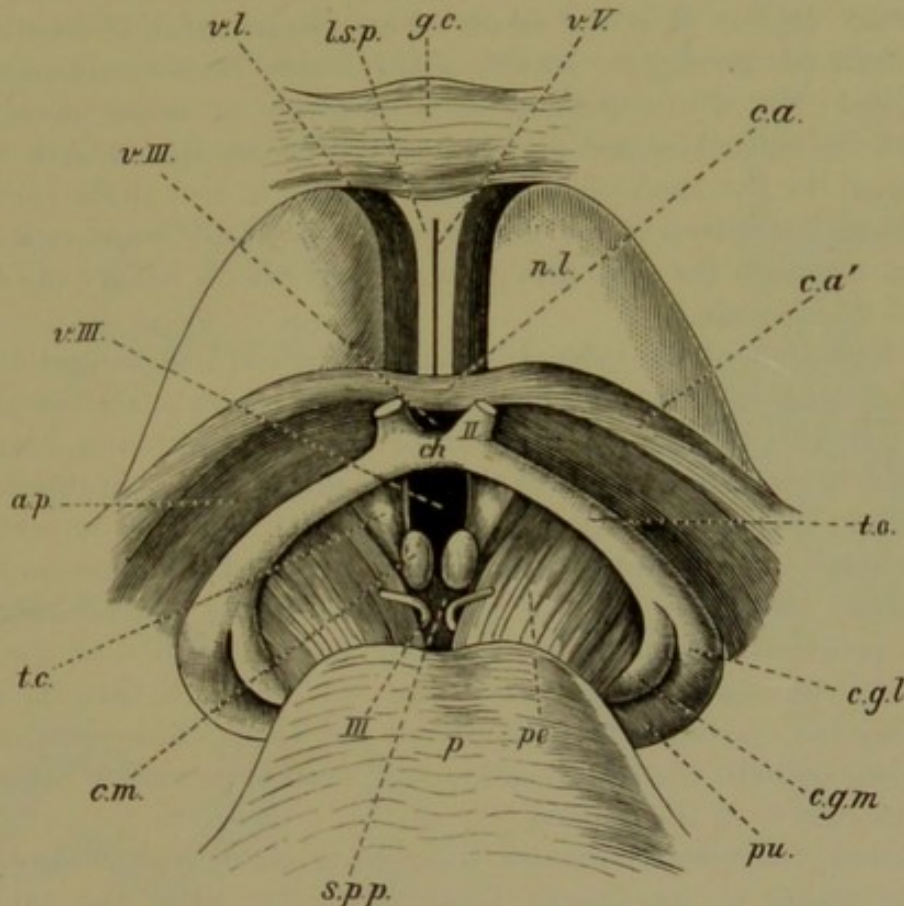


Fig. 220.—Diagrammatic view of the under side of the brain, after *Schwalbe*. In front of the optic tracts the superficial substance of the base of the brain has been dissected away so as to expose the ansa peduncularis, anterior commissure, and basal aspect of the nuclei lenticulares.—*l.s.p.*, Septum pellucidum; *v.l.*, anterior horn of lateral ventricle; *n.l.*, nucleus lenticularis; *c.a.*, anterior commissure; *c.a'*, twisted portion of ditto; *v.III.*, third ventricle; *g.c.*, genu corporis callosi; *c.g.m.*, corpus geniculatum mediale; *c.g.l.*, corpus geniculatum laterale; *c.m.*, corpus mammillare; *pu.*, pulvinar; *v.V.*, fifth ventricle; *II*, optic nerve; *ch*, chiasma nervorum opticorum; *t.o.*, tractus opticus; *t.c.*, tuberculum cinereum; *III*, oculomotor nerve; *s.p.p.*, substantia perforata posterior; *pc*, pedunculus cerebri; *p*, pons.

*Blattmann*, and *Reissner* had found it. In fishes, the commissures appear to be fused, so that no distinction between the corpus callosum and anterior commissure is possible. *Osborn* believes that both commissures exist in reptiles, birds, and amphibia, although in the two former classes the corpus callosum, owing to the rudimentary condition of the cortex in these animals, is very ill-developed. But the fact that no corpus callosum is present in any monotreme or marsupial, throws great doubt upon the homology of the commissure which is supposed to represent it in sub-mammalian



vertebrates. Its occasional absence from human brains also proves its late appearance in the phylogenetic series. The cerebral hemisphere of the bird, and to a less extent of the reptile, is homologous, not with the entire hemisphere of the mammal, but, as pointed out by *Cuvier*, with little more than the corpus striatum.

Even in post-embryonic life there is some indication of a shifting round of the hemisphere. The fissure of Rolando is nearer to the coronal suture in the child than it is in the adult. This displacement is attributed by *Cunningham* to the slighter growth of the frontal bone as compared with the parietal; but if the parietal bone takes on an undue share of the growth of the calvarium, the parieto-occipital fissure should shift forward with regard to the lambdoidal suture, whereas it also shifts backwards. Rather there is evidence of the slower growth of the calvarium relatively to the brain, although the skull also, to a certain extent, follows the shifting round of its contents.

The disposition of the veins of the hemisphere and the changed direction which they assume during development strongly supports, as *Browning* has pointed out, the theory of a rotation of the brain within its case. The veins which open into the front of the longitudinal sinus join this vessel at right angles; those which open into its posterior end have an extremely oblique course. They discharge their blood under what appears to be very unfavourable conditions, against the stream in the large vessel. The obliquity progressively increases, according to the position of the veins, from before backwards. It increases from early foetal life until the growth of the brain has ceased. The obliquity of the veins which open into the venæ Galeni beneath the corpus callosum is even more marked than in the case of the vessels on the surface.

ONTOGENY.—Evidence obtained from direct observation of the brain in successive stages of its growth must obviously, when the subject is thoroughly worked out, be the first to be submitted in proof of the rotation of the hemisphere. As yet, however, our knowledge of this subject is very incomplete, owing in part to the absence of research, in part to the special difficulties dependent upon the nature of the tissue of which the brain is composed. Unlike other tissues of the body, the nervous tissue is peculiarly plastic. In the course of its growth it may receive marks of torsion and other displacements, but, while elsewhere such marks remain permanently, in the brain they are obliterated by further growth. The manner in which its mass is added to also has an important bearing upon its form. It must be remembered that only the cellular elements enter into its original constitution; the fibres are but processes of the cells. Of the primitive epiblastic cells involuted to form the nervous tube, some are favoured above the rest and become the functional nervous elements, while to the others only subsidiary, supporting, nutritive, and insulating functions are assigned; the latter become the neurogleia and myelin-cells; just as in the case of each little group of epithelial cells involuted into a follicle of the ovary, one only becomes an ovum, the others minister to its wants. It may be, therefore, that the line along which a nerve-fibre is to grow is laid



down, before the fibre itself appears, by the chain of accessory cells which have taken up their position along its route; or, on the other hand, it is open to us to suppose that the route chosen by a fibre depends upon convenience at the time of its appearance, and that the marshalling of the myelin-cells in files results from some stimulus which the growing fibre affords. If, owing to a displacement of the cortex, it can reach its destination by a shorter route than the tract occupied by neighbouring fibres, which being fully developed at the time of the rotation of the brain, shared in the displacement of the cortex, it is open to it to leave the original tract, and thus the primitive arrangement of the constituent parts of the brain may be masked. Despite, however, the obliteration of the indications of

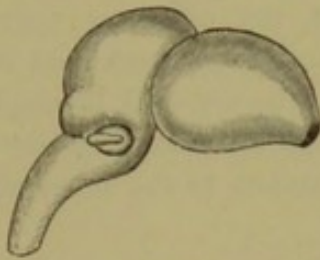


Fig. 221.—Early foetal brain.

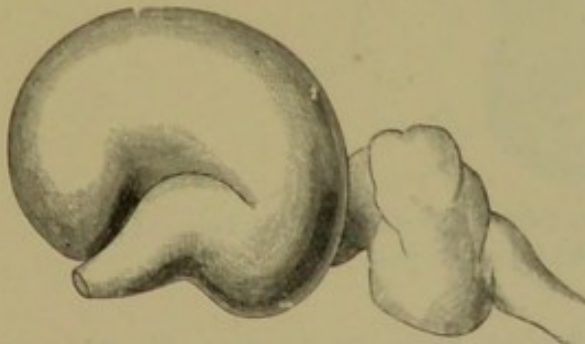


Fig. 222.—Brain of foetal sheep in which the rhinal fissure is developed and separates the pyriform lobe from the rest of the cerebrum. Its distinctness is exaggerated in the wood-cut.

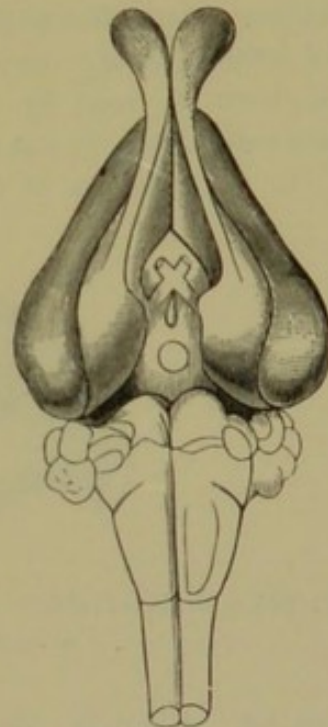


Fig. 223.—Diagrammatic view of the under surface of the brain of a young rabbit.

rotation which these two causes are likely to produce, we still can see in the changes of form which the great brain undergoes appearances suggestive of rotation. This, at least, is the conclusion likely to be drawn from the examination of three such pictures as are here inserted.

In fig. 221, copied from Löwe,\* a very early stage in the growth of the brain is shown; the hemisphere is directed forwards and bears the olfactory bulb at its anterior end. Fig. 222 represents the appearance presented by almost every mammalian brain after the formation of the rhinal fissure. The olfactory bulb is now attached to the extremity of the pyriform lobe, and the suggestion of a folding-over of the whole hemisphere is very strong. The pitting of the side of the brain, due to the

\* Löwe, *Entwicklungsgeschichte des Nervensystems*, Pl. I. figs. 1 and 2.



tension on its posterior end produced by the attachment of the olfactory bulb to the cribriform plate, is beginning to appear as the fossa of Sylvius. Fig. 223, again after Löwe, is inserted for the purpose of showing the continuity of the olfactory bulb, pyriform lobe, and gyrus uncinatus in a rabbit's brain. Fig. 224 shows the hippocampus exposed from above by cutting away the roof of the lateral ventricle. It is curious to notice how the backward growth of the hemisphere increases the size of the loop. In the brain of a sheep, for instance, the fimbria (posterior pillar of the fornix) is transverse at its first appearance. The higher the animal in the mammalian scale, the more nearly does its fornix-system assume a longitudinal direction.

Of the earliest stages of the growth of the brain we have very few observations, but *Marshall's* discovery that the olfactory nerve arises, like all other sensory nerves, from the neural ridge, and that it is then pushed down in front by the outgrowth of the cerebral hemispheres, to be again caught up in the cortex mantle, opens up great possibilities with regard to the relation of the olfactory apparatus to the hemisphere, and

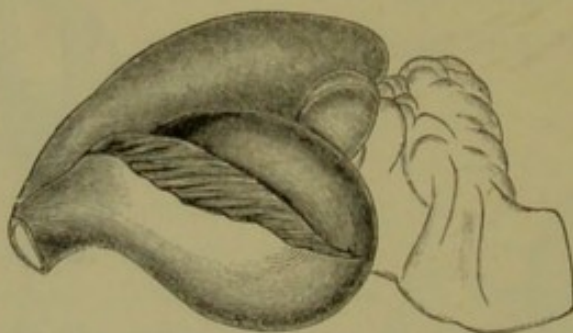


Fig. 224.—Brain of rabbit. The upper part of the cerebrum has been cut away so as to expose the hippocampus.

prepares us, although the research has gone no further, to find an arrangement in the first nerve quite unlike that of the others.

**PHYLOGENY.**—The reference already made to the marsupial brain has drawn attention to the fact that in lower mammals the rotation has gone less far than it has in the higher members of the class. Whether or not it is a phase in the development of any sub-mammalian animals, we are not prepared to state. Certain it is that, if we descend as far as the reptiles, rotation is out of the question. As already pointed out, the reptilian brain, like the brain of the early mammalian embryo, is directed forwards, its ventricle communicating at the back with the third ventricle through the foramen of Monro, and ending in the ventricle of the olfactory bulb in front. The great gap between the bird's and the mammal's brains, although bridged over by the brain of the monotreme, renders it difficult to point out the first animal in which the brain has adopted a looped disposition. The peculiar deficiency of cortex in the bird's brain renders rotation unnecessary, since the reason for rotation is not far to seek. If we compare such an extreme type as the crocodile with any mammal, we notice a contrast in the whole architecture of the head. The reptilian



head is directed forwards; is elongated in the direction of the axis of the body. The mammalian head approaches a globular form. With the greatly increased size of the cerebrum as we ascend in the vertebrate scale, economy of space for its reception becomes necessary. Doubtless, for other reasons also, a shortening of the head is desirable, and the larger brain can only be packed inside the shorter skull by throwing its hemispheres over into loops.



## GLOSSARIAL INDEX.

*German names with the English equivalents used in this translation.*

*Latin and English names for parts of the central nervous system with common synonyms and their German and French equivalents.\**

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<b>Adergeflechte des Grosshirns</b> , choroid plexus.			
„ „ <b>Kleinhirns</b> , choroid plexus of cerebellum.			
<b>Adergeflechtfurche</b> , choroidal fissure, transverse fissure.			
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<b>Aeussere Kapsel</b> , external capsule.			
<b>Aeusserer Kern der Keilstränge</b> , nucleus funiculi cuneati.			
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<b>Akusticushauptkern</b> , auditory nucleus, chief.			
<b>Akusticus Kern accessorischer</b> , auditory nucleus, accessory.			
„ <b>grosszelliger</b> , auditory nucleus, large-celled.			
<b>Akusticuswurzel</b> , aufsteigende, auditory root, ascending.			
„ <b>laterale</b> , auditory root, lateral.			
„ <b>mediale</b> , auditory root, mesial.			
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\* No attempt has been made to render this Glossary complete. French terms are not given when their form of expression is very similar to English.







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„ <b>weisse</b> , white commissure in floor of the third ventricle.	
<b>Bogenbündel des Grosshirns</b> , fasciculus arcuatus.	
„ <b>der Medulla oblongata</b> , fibræ arcuatæ.	
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<b>Brückenfasern</b> , fibres of the pons.	



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- Vorderhorn des Rückenmarks, cornu anteriorus.  
 „ „ Seitenventrikels, anterior horn of lateral ventricle.  
 Vordersäule, anterior columns of grey matter of spinal cord.  
 Vorderseitenstrangreste, rest of or continuation upwards of the anterior and lateral columns.  
 Vorderstrang, anterior white column.  
 Vorderstranggrundbündel, ground-bundle of the anterior column.  
 Vormauer, claustrum.  
 Vorzwickel, præcuneus.  
 Voûte à trois piliers, fornix. See *Fornix*.

## W

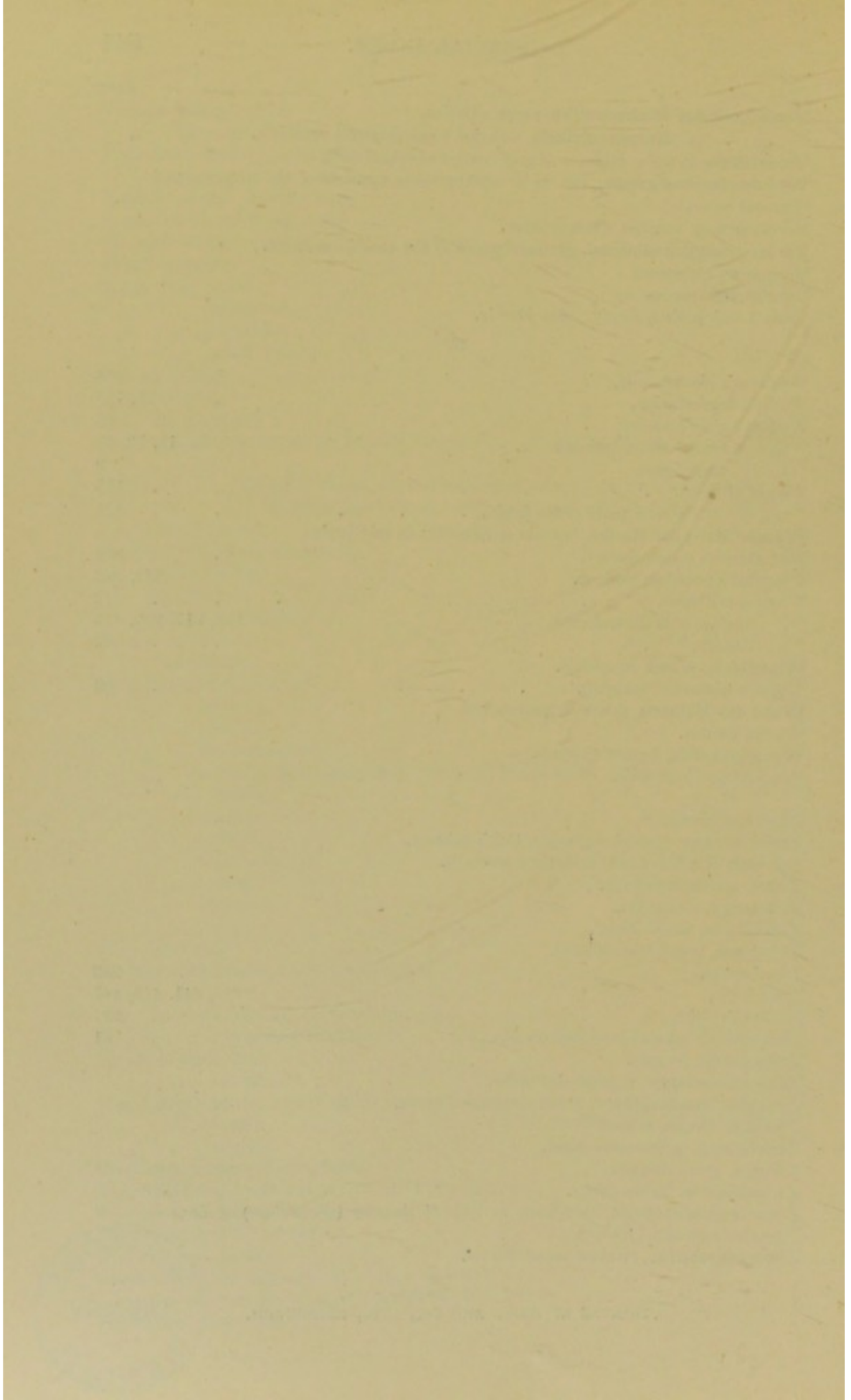
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 Zirbel, glandula pinealis.  
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 Zwickel, cuneus, *le coin*.  
 Zwickelstiel, pedunculus cunei.  
 Zwinge, gyrus cinguli.  
 Zwischenhirn, 'tween-brain.  
 Zwischenmarkscheide, membrane at node of Ranvier (*Obersteiner*) at Lantermann's segments (*Kuhnt*).  
 Zwischenschichte, stratum intermedium.

















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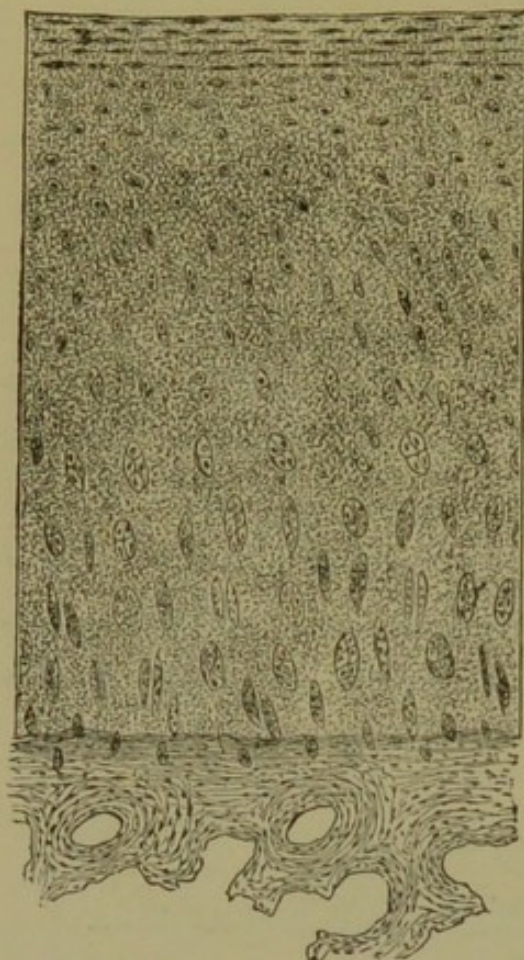


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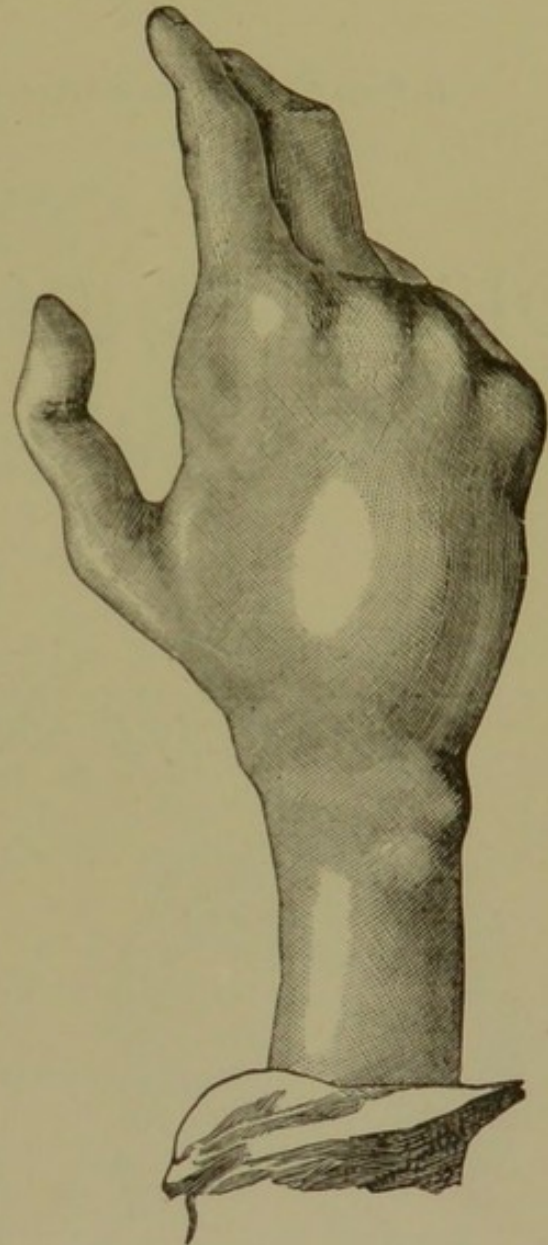


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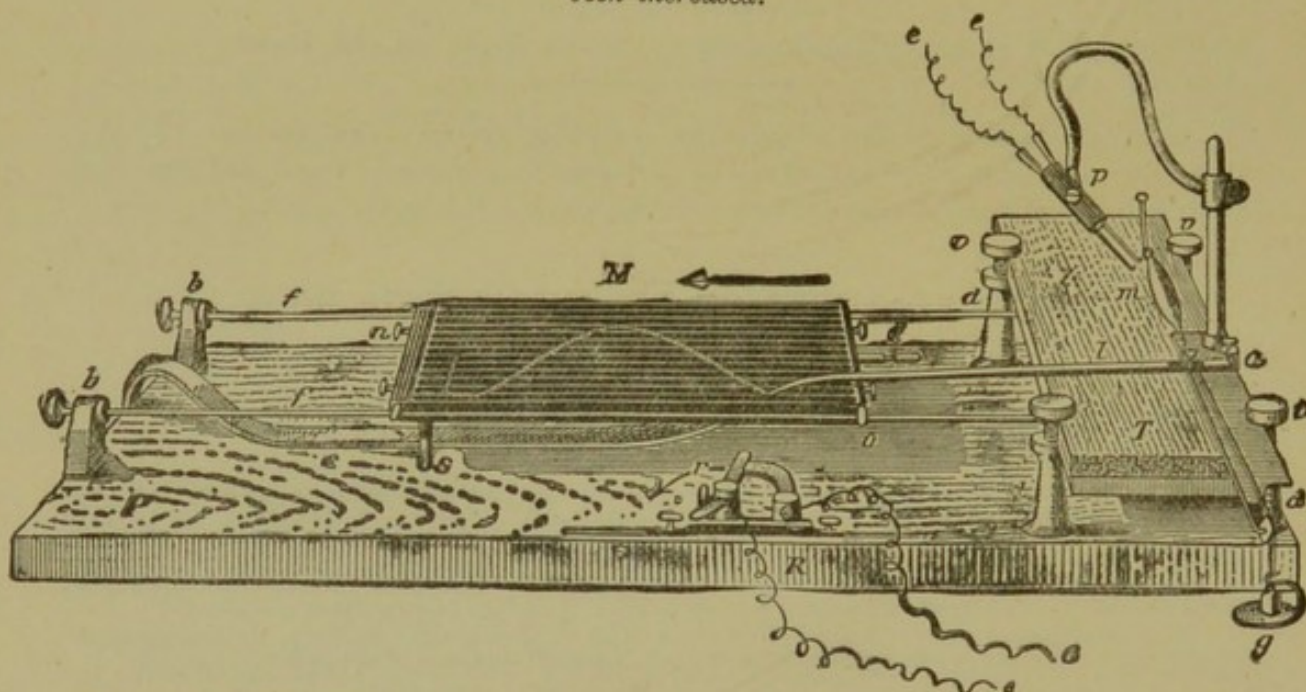


Fig. 118.—Horizontal Myograph of Frédéricq. *M*, Glass plate, moving on the guides *f, f*; *l*, Lever; *m*, Muscle; *p, e, e*, Electrodes; *T*, Cork plate; *a*, Counterpoise to lever; *R*, Key in primary circuit.

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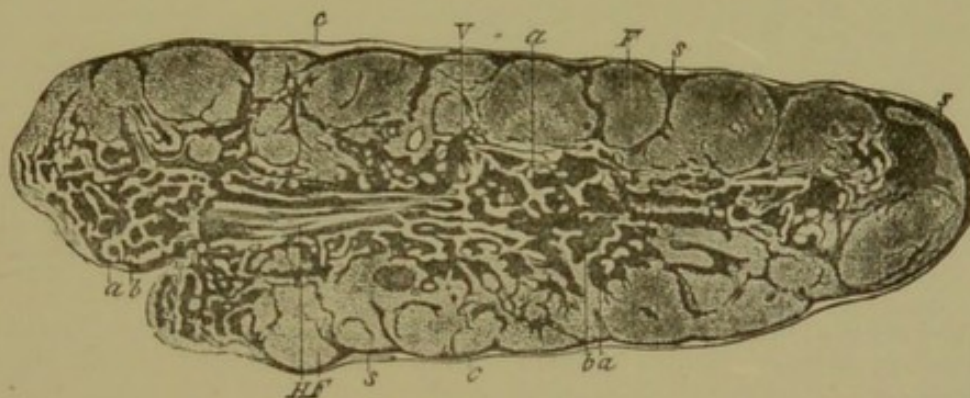


Fig. 200.—L.S., Cervical Ganglion of Dog. *c*, Capsule; *s*, Lymph sinus; *F*, Follicle; *a*, Medullary cord; *b*, Lymph paths of the medulla; *V*, Section of a blood-vessel; *HF*, Fibrous part of the hilum,  $\times 10$ .

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
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