FINER ANATOMY

OF THE

CENTRAL NERVOUS
SYSTEM

AN INTRODUCTION TO THE

FINER ANATOMY

OF THE

CENTRAL NERVOUS SYSTEM

BASED UPON THAT OF THE

ALBINO RAT

WITH TWENTY-EIGHT PLATES AND TEN ILLUSTRATIONS
IN THE TEXT

BY

E. HORNE CRAIGIE, Ph.D.

ASSISTANT PROFESSOR OF COMPARATIVE ANATOMY AND NEUROLOGY
IN THE UNIVERSITY OF TORONTO

PHILADELPHIA

P. BLAKISTON'S SON & CO.

1925

PREFACE

SEVERAL guides for the study of the gross anatomy of the brain have been published but up to the present time there has been available no small handbook devoted to the minute anatomy of the nerve centres and pathways—which is at least as important as the gross anatomy —in any laboratory animal. The present text is an attempt to fill this gap—to provide a brief but comprehensive introduction to the functional anatomy of the central nervous system of a common laboratory type of size convenient for the use of serial sections.

As the book is designed primarily for elementary students, all important differences from the human structure (which are not very numerous but are sometimes quite instructive) are pointed out, and an introductory chapter upon the general principles of nervous structure has been included, as also an appendix outlining a simple form of the Weigert method of preparing sections. From two or three brains enough short series of sections for a fair sized class may be made.

Besides being a suitable form for didactic purposes, the rat is so widely used in research that an atlas of the anatomy of its central nervous organs and a summary of what has been recorded regarding them should be valuable to many investigators. With this end in view, an attempt has been made to include all details of the neuro-anatomy of this type which are to be found in the literature except those of the histological localization in the cerebral cortex. Such details are set in small type when they are not of immediate importance to the elementary student. A bibliography has been added to bring up to date, so far as the central nervous system

is concerned, that published by Donaldson in 1915. It is hoped that it has been possible in this way to provide a useful manual for research workers without lessening the value of the book as an introductory text.

Special acknowledgements are due to Dr. Henry H. Donaldson. The author is indebted also to Dr. B. A. Bensley, to Dr. J. W. Papez, who kindly sent him manuscript notes of his observations upon the brain of the rat, to Dr. C. Judson Herrick for reading the manuscript, for the sketch upon which Fig. 6 is based, and for permission to use Fig. 5, to Dr. J. B. Johnston for Figs. 7 and 8, to Dr. Æ. B. Droogleever Fortuyn for Fig. 10, and to the W. B. Saunders Co. for Figs. 1 and 4.

E. HORNE CRAIGIE.

University of Toronto,
      June, 1925.

CONTENTS

25213

CHAPTER I.

Gross Anatomy of the Central Nervous System.

WHILE the gross features of the brain may be studied a little more conveniently if a larger type than that of the rat is employed, the latter nevertheless shows most of the important structures very satisfactorily.

The spinal cord extends through the vertebral canal from the base of the skull to the sacral region. It is roughly cylindrical, but presents two slightly swollen regions which are somewhat depressed. These are the cervical and lumbar enlargements, from which arise respectively the nerves for the fore and hind limbs. Posteriorly, it tapers off to end in the sacrum in a fine thread, the filum terminale, which runs back for some distance in the tail. From the spinal cord arises a series of paired spinal nerves, the first of these emerging between the skull and the first vertebra, while the remainder emerge between successive vertebrae. In the cervical region, all the nerves except the last are named from the vertebrae in front of which they emerge, but the nerve behind the last cervical vertebra is also reckoned to this region, so that while there are seven cervical vertebrae, there are eight pairs of cervical nerves. Each of the remaining nerves is named from the vertebra behind which it emerges. Thus there are thirteen pairs of thoracic nerves, six pairs of lumbar nerves, four pairs of sacral nerves, and three pairs of caudal nerves.

Each spinal nerve is attached to the cord by dorsal and ventral roots, and on the former may be observed a slight enlargement, a spinal ganglion or dorsal root ganglion. Similar masses occur near the bases of some of the cranial nerves, the

cerebral ganglia, though the latter are not very evident in gross dissection.

An almost imperceptible dorsal median sulcus (sulcus medianus posterior) runs along the dorsal middle line and a deep groove, the ventral median fissure (fissura mediana anterior), occurs in the corresponding position ventrally. A short distance to each side of the dorsal median sulcus is another fairly distinct groove, in which the dorsal roots of the spinal nerves enter the cord. This is the dorso-lateral sulcus (sulcus lateralis posterior). The line of attachment of the ventral roots is indicated by a much fainter depression, the ventro-lateral sulcus (sulcus lateralis anterior).

A dorsal view of the entire brain (Plate I.) shows the three primary subdivisions, the cerebral hemispheres not being sufficiently developed in the rat to conceal entirely the more posterior sections. Anteriorly, the forebrain or prosencephalon is represented by the cerebral hemispheres and the olfactory bulbs; posteriorly, the hindbrain or rhombencephalon is represented by the cerebellum and the medulla oblongata; while between the cerebral hemispheres and the cerebellum, appear the posterior colliculi of the midbrain or mesencephalon.

In the hindbrain, the cerebellum appears as a massive thickening of the roof in the anterior part of the region, which has attained so great a size as completely to conceal the large cavity of the hindbrain, the fourth ventricle. Its surface is thrown into numerous transverse folds, and shows a division into different regions, of which the conspicuous ones are the median vermis, the large paired cerebellar hemispheres (lobuli ansiformes), at each side of it, and the small, stalked floccular lobes projecting laterally. The visible part of the floccular lobe is the paraflocculus, which forms the greater part of this lobe in the rodent, the flocculus being only an inconspicuous lobule at the base of the stalk.

The cerebellar hemisphere represents only a part of the much larger hemisphere of man.

The cerebellum consists morphologically of three lobes, anterior, middle, and posterior, the fissures separating them being the sulcus primarius and sulcus praepyramidalis respectively (see Fig. 3). The anterior lobe consists of four transverse lobules, but only the last of these can be seen from the dorsal surface. The posterior lobe is composed of a median part and the lateral floccular lobes, the median part being made up of pyramis, uvula, and nodulus (named dorso-ventrally), of which only the pyramis and the large uvula behind it appear from above. The middle lobe likewise consists of median and lateral portions, the lateral ones being the hemispheres, all of which are divided by transverse grooves into narrow gyri.

The cerebellum may be removed by carefully cutting through the peduncles which attach it to the medulla oblongata at each side. When this is done the cerebellum is found to constitute only a very narrow transverse strip of the actual roof of the ventricle below it. The greater part of the ventricle is roofed by two membranes attached to the cerebellum along this strip and extending forward (velum medullare anterius or anterior medullary velum) and backward (velum medullare posterius or posterior medullary velum) to the extremities of the widely open fourth ventricle. The posterior medullary velum contains greatly convoluted groups of blood vessels which project into the ventricle, pushing the velum before them—these vessels forming the chorioid plexus of the fourth ventricle.

The trochlear nerve (IV) decussates in the anterior edge of the anterior medullary velum and may be seen emerging round the postero-lateral aspect of the midbrain.

The middle cerebellar peduncle, which has been cut through, extends straight ventrally and forms a thick transverse mass of fibres crossing the most anterior part of the

ventral surface of the hindbrain—the pons (pons Varolii). Immediately behind this (Pl. II.) is another, much less distinct transverse band, the trapezoid body. This shows at each side of the middle line a marked elevation, which is the anterior end of a distinct ridge, the pyramid, extending along each side of the ventral median sulcus from the lower end of the medulla oblongata up to this point, where the sulcus itself is obliterated by the transverse fibres.

Coming back to the dorsal surface, the large fourth ventricle or rhomboid fossa may now be studied (Pl. III.). This cavity narrows anteriorly into the aqueduct of Sylvius, the cavity of the midbrain, and posteriorly into the central canal of the spinal cord. A narrow deep posterior median sulcus runs along the floor of the ventricle in the middle line, and for about half the length of the ventricle a narrow, low ridge, the funiculus teres, bounds this fissure at either side. Just in front of this ridge the floor of the ventricle forms a considerable eminence at each side, under which lies the genu of the facial nerve (p. 48) and which is consequently called the colliculus facialis. In front of this, a very slight pit at each side of the ventricle is the fovea superior. On a level with the funiculus teres appears a pair of large rounded lateral elevations, which contain the vestibular nuclei. The slight lateral pit at the posterior end of this eminence is the fovea inferior. The triangular formation at the posterior extremity of the ventricle is the calamus scriptorius.

The medial parts of the dorsal columns of the spinal cord (funiculi graciles) end in a pair of enlargements, the clavae, which are spread apart by the ventricle, and in front of each of these the thick wall lateral to the vestibular nucleus is formed by the restiform body or inferior cerebellar peduncle. In the cut surface of the peduncles, this body, the middle peduncle or brachium pontis, and the superior peduncle or brachium conjunctivum can all be distinguished. The last

of these forms the lateral wall of the anterior part of the ventricle.

Immediately behind the cut part of the peduncles, crossing the restiform body, is a transverse ridge, the tuberculum acusticum, which appears to become continuous ventro-laterally with the eighth or auditory nerve. Anterior and ventral to this, the facial nerve (VII) emerges from the side of the medulla, and just anterior to it again is the root of the trigeminal nerve (V), in which large, sensory and small, motor parts may be distinguished.

In order that the midbrain may be observed the posterior dorsal portions of the cerebral hemispheres must be raised and pressed apart. This reveals two pairs of rounded eminences, the corpora quadrigemina, which make up the dorsal part of the midbrain. The ventral part is considerably narrower antero-posteriorly than is the dorsal part, so that the region is somewhat wedge-shaped. As seen from below, it appears in a depression between the pons behind and the cerebral hemispheres and mamillary body in front. A pair of massive longitudinal fibre-tracts, the pedes pedunculi cerebri, converge from the hemispheres and disappear under the pons, covering the whole ventral aspect of the midbrain except a median hollow between them, the interpeduncular fossa. Through each peduncle emerges the oculomotor nerve (III).

In the forebrain—indeed in the brain as a whole—the most conspicuous structures are the large cerebral hemispheres, which in the rat and other small animals have smooth surfaces, but which in the larger mammals are greatly convoluted. The hemispheres of the rat are much smaller proportionately than those of man and the higher mammals. They are separated by a deep median cleft, the longitudinal cerebral fissure.

At the front of each hemisphere lies the olfactory bulb, in which end the numerous fine strands of the olfactory nerve

(I). Running back from this on the ventral surface is a narrow, white band, the olfactory tract (Pl. II.). The ventral part of the hemisphere, along which the olfactory tract runs, is marked off by a longitudinal groove, the rhinal (or limbic) fissure, which separates this region (the olfactory lobe) laterally from the more dorsal parts of the hemisphere. The gray matter subjacent and lateral to the olfactory tract forms the lateral olfactory gyrus, which enlarges posteriorly into the pyriform lobe, while the rounded gray mass medial to the tract is usually known as the tuberculum olfactorium, though it represents also the anterior perforated area (see p. 91). The superficial part of the brain dorsal to the rhinal fissure is entirely non-olfactory in its relations, and is known as the neopallium.

If the hemispheres be pressed apart so as to open up the longitudinal cerebral fissure, a broad white band is seen connecting them. This is the corpus callosum.

Projecting between the dorsal posterior poles of the hemispheres and lying in the furrow between the superior corpora quadrigemina, is the pineal body, a small gland attached by a stalk to the unpaired part of the forebrain, the diencephalon. The latter may be exposed by raising, or better by cutting away the back parts of the hemispheres. The stalk of the pineal body is attached to the extreme posterior portion of the membranous roof of the cavity of the diencephalon, the third ventricle. This roof, like that of the fourth ventricle, contains a chorioid plexus, and must be removed to expose the ventricle. The latter is almost completely obliterated by the fusion of its lateral walls over the greater part of their area, forming the soft commissure or intermediate mass. The dorsal part of the ventricle is bounded at each side by a conspicuous longitudinal ridge, the habenula, the posterior ends of the two habenulae being connected by a thin curved band, the habenular commissure. Lateral to this, the wall is extremely massive, containing the thalamus

and related parts (chapter XIII). Two eminences appear on its lateral surface, the smaller, posterior one being the medial geniculate body, the larger, anterior one the lateral geniculate body, and in front of this the diencephalon is attached laterally to the cerebral hemisphere (corpus striatum). A deep, oblique groove, into which fits the fimbria of the hippocampus (vide infra), marks roughly the boundary between thalamus and corpus striatum on the dorsal surface.

The lateral geniculate body is covered with white fibres of the optic tract, which may be followed down and forward to the optic chiasma, the decussation on the ventral surface of the brain of the two optic tracts. From the chiasma the tracts continue forwards as the optic nerves.

Behind the optic chiasma lies the pituitary body, or hypophysis, which is attached to the base of the brain by a thin, hollow stalk, the infundibulum. The hypophysis is frequently left behind when the brain is removed from the skull, the infundibulum being broken through, in which case the cavity of the infundibulum appears as a small median slit opening into the third ventricle. This slit is surrounded by an elevation of gray matter, the tuber cinereum, and this is continuous posteriorly with the mamillary body, a conspicuous mass projecting postero-ventrally over the anterior part of the interpeduncular fossa. There are paired mamillary bodies in the human brain, but in the rat they are represented by a single median mass.

If one hemisphere be removed, there may be observed on the part of its medial surface which lies in contact with the diencephalon a distinct curved groove, the hippocampal fissure, and parallel and a little anterior to it a conspicuous ridge of white fibres, the fimbria hippocampi (Pl. IV.). Between these is a fainter groove, which marks the division between the fascia dentata or dentate gyrus, lying between it and the hippocampal fissure, and the hippocampus proper, covered with a thin layer of white fibres which join the

fimbria. The dorsal end of this (the postcommissural) part of the hippocampal formation is connected posteriorly through the gyrus subsplenialis with a narrow ridge, the fasciola cinerea. This, in turn, curves round the splenium of the corpus callosum and runs forward as the very thin gyrus supracallosus or indusium griseum. All these structures are illustrated in Pl. IV.

Scraping away the gray matter, or cerebral cortex, from the dorsal part of the hemisphere reveals the white fibres of the corpus callosum, and this also may be removed so as to expose the cavity of the hemisphere, the lateral ventricle. The postero-medial part of the floor of the ventricle is formed by a curved ridge, the hippocampus, while the small antero-lateral portion appears as a convex mass, part of the corpus striatum. Between these projects the chorioid plexus of the lateral ventricle. This is continuous with that of the third ventricle through the foramen of Monro or interventricular foramen, which connects these ventricles. In front of the foramen, the medial wall is formed by the septum.[1]

Division of the brain in the median plane reveals another instructive view, showing to particular advantage the larger commissures and the relations of the ventricles, besides other features. In addition to the commissures already mentioned, there may be observed the hippocampal commissure, which appears as a thin flat band directly ventral to the posterior part of the corpus callosum with a thickened anterior portion; the anterior commissure, a distinct cylindrical strand crossing in the anterior wall of the third ventricle (the lamina terminalis); and the posterior commissure, a less conspicuous structure just below the habenular commissure (Pl. IV., XXVI.).

FUNDAMENTAL STRUCTURE OF NERVOUS ORGANS.
PRINCIPLE OF NERVE COMPONENTS.

THE nervous system is made up of cells which fall into two categories—those which perform the characteristic nervous functions and those which do not. The cells of the latter class, the neuroglia cells, are mainly supportive in function and form a framework in which lie the cells of the former group, the true nerve cells or neurons. There are also strands of ordinary connective tissue extending into the substance of the nervous organs from the membranes which cover them, usually accompanying blood-vessels.

The neurons vary considerably in form and in structural details, but the typical neuron consists essentially of a cell body or perikaryon, a varying number of branched receptive processes, the dendrites, and a single efferent process, the axon, axis-cylinder, or neurite. The axon frequently has a sheath of fatty material (myelin), the myelin (medullary) sheath, and may give off small branches, usually perpendicular to the main fibre, the collaterals. The nerve cells pass their impulses from one to another through connections known as synapses. The essential structure of the synapse is still the subject of dispute, but it is usually held to be simply a point of close contact, without actual continuity, between the terminal of an axon and the next cell. The details of structure of the nerve cell are described in practically all text-books on the anatomy or physiology of the nervous system and will not be considered here.

The perikarya of the afferent neurons are nearly always situated outside the central nervous organs, where most of

them are grouped in small masses, or ganglia. As noted in
the previous chapter, a ganglion occurs on the dorsal root of
each spinal nerve and near the bases of some of the cranial
nerves—*i.e.*, near the point of entry into the central system
of every afferent nerve. These perikarya have certain
peculiarities of form, and it has been shown that in the rat
their volume varies during growth in direct proportion to
the area or skin-surface of the animal. This relation is con-
sidered to be an adaptation for maintaining the sensory
discrimination despite the extension during growth of the
area supplied by a single neuron.[1]

The main functional unit in the nervous system is a chain
of such neurons consisting in the simplest possible condition
of two elements—a receptive, sensory, or afferent cell, which
receives a stimulus at the periphery and conducts the result-
ing impulse to the central organ, and a motor or efferent
cell, which is stimulated by the impulse in the afferent neuron
and transmits the resulting impulse to a muscle. The muscle
thus brought into action is termed the effector, while the
chain of neurons is called a reflex arc. It is the mechanism
which brings about that immediate, involuntary response
to a stimulus which is known as a reflex action.

Seldom, if ever, does the reflex arc consist of only two
neurons. There is practically always at least one internuncial
neuron between the afferent and efferent elements, and in
the great majority of cases there are many more. The whole
nervous system is made up of an infinitely complex system
of such arcs variously connected and superposed.

The internuncial neurons frequently are connected with
several other cells from which they receive stimuli, often of
different kinds, so that the impulse in such an element may
be the resultant of several stimuli instead of the effect pro-
duced by a single one. The internuncial cell thus becomes a
correlation neuron, and a group of such cells is a correlation

[1] Donaldson and Nagasaka, 1918.

centre, if the various stimuli received are of different kinds. A correlation neuron may send its impulses to several other elements, which may include both efferent cells and other correlation neurons. Thus one correlation centre may influence another, and it itself may be controlled by yet another, and so on. Hence we have lower and higher functional levels in the central nervous system, the lowest being the simple reflex level, the higher the correlation levels, of which there are many, and the higher levels exerting a directing or controlling influence over the lower ones. To a certain extent these correspond roughly with the structural levels, the simple reflexes being confined to the lower parts of the brain and to the spinal cord, while only the lower correlation centres are found near these, the higher ones occurring in more or less regular succession towards the upper or anterior part of the brain, and the highest being in the cerebral cortex.

Any part of the nervous system which is composed chiefly of cell bodies and dendrites or unmyelinated axons appears rather grayish in the fresh condition and hence is known as gray matter, while the presence of a large number of axons with myelin sheaths (myelinated fibres) gives a region a clear white colour, so that it has received the name of white matter.

In all parts of the system, neurons of similar function tend to be associated topographically. Hence we find more or less definite groups of cells, or masses of gray matter, which are concerned with particular functions and which are given the name of nuclei. The axons proceeding from a particular nucleus or group of nuclei also associate themselves into definite groups which are called fibre-tracts, when all the fibres have similar connections. A bundle containing fibres belonging to more than one tract is called a fasciculus. It is the task of neuro-anatomy to identify the various nuclei and tracts, showing how they are related, both structurally and functionally, and to trace out in detail the

pathways of the excitations which constitute or underlie all nervous functions.

One of the most fruitful conceptions which have been brought to bear upon the study of the structure of the central nervous system is that of functional components, which has made possible the analysis upon a functional basis of the main patterns in the almost inconceivably complex system of nerve centres and tracts which confronts the student of the finer anatomy of the brain. According to this principle, all peripheral nerve fibres may be divided into four groups according, first, to whether they conduct impulses towards (afferent) or away from (efferent) the central nervous system; and, second, to whether they connect at the periphery with somatic or visceral structures. Moreover, while this suffices for a complete classification of the fibres in the spinal nerves, each of these groups as it occurs in the cranial nerves may be subdivided into two components—general and special— according to whether the structures innervated have changed greatly from their primitive condition or not—e.g., the simple nerve endings in the intestine belong to the general visceral components while the gustatory fibres are special visceral sensory. Thus the cranial nerve components are eight[1] in number:—general and special somatic afferent, general and special visceral afferent, general and special somatic efferent, and general and special visceral efferent.

The importance of this analysis from the standpoint of neuro-anatomy is due to the fact that these different components, having been identified at the periphery, can be traced into the brain, where they are found to connect with distinct centres of gray matter, or nuclei. The fibres arising in these nuclei may thus be recognized as secondary fibres of the particular functional type being studied, and these

[1]Actually only seven of these are found in the cranial nerves of mammals, the general somatic efferent group being confined to the spinal nerves.

may be followed to their termination in secondary nuclei. Thus the analysis may be continued until the various components are found to end in centres common to two or more of them—correlation centres, and from these, connections may be followed to higher correlation centres, and the functional pattern of the whole brain may be elucidated.

This principle is of value not only to the research worker, but also to the beginning student, whom it provides with what is probably the best available line of attack in approaching a difficult subject. Experience has shown that the most satisfactory way of making a first study of the finer anatomy of the brain is not to study each section as a whole but to follow out each functional system through the series of available sections, completing its examination before looking at the elements belonging to another system. This method of presentation will accordingly be employed in the following pages.

CHAPTER III.

The Spinal Cord.

IN transverse sections, the spinal cord shows a large mass of
gray matter surrounding the central canal, with white
matter disposed outside it. The shape of the section as
a whole and the shape of the mass of gray matter vary some-
what according to the level of the cord from which the section
is taken, the relative areas of gray and white matter also
varying (see Pl. V.). The gray matter, however, always
appears in transverse sections to have roughly the shape of
the letter H. The afferent nerve roots enter the cord opposite
the dorsal horn of the H, or *dorsal column of gray matter
(cornu dorsalis)*, while the efferent fibres arise from cells in
the ventral horn, or *ventral column of gray matter (cornu
ventralis)*, and leave the cord opposite it. The superficial
part of the dorsal column is distinct from the rest, having a
clearer appearance, and is known as the *gelatinous substance
of Rolando (substantia gelatinosa Rolandi)*. This is very
massive in the rat, where it does not vary very greatly in
shape at different levels of the cord, as in man and many
other animals, but forms a broad, thick cap over the under-
lying parts.

The section is divided into lateral halves by the deep
fissure which runs along the ventro-median aspect of the cord
(*ventral or anterior median fissure*) and the shallow dorso-
median fissure, which is continued in towards the central
canal by a sheet of connective tissue, the *dorsal or posterior
median septum*. In each of the lateral halves thus formed,
the white matter is further divided by the gray columns and
the nerve roots into *dorsal*, *lateral*, and *ventral funiculi*. The

line of entry of the dorsal roots is marked by a superficial groove, the *dorso-lateral groove*, and between this and the dorsal median fissure is an *intermedio-lateral groove*, from which also a connective tissue septum extends inward. The last mentioned septum, which appears only in the upper levels of the spinal cord, divides the dorsal funiculus into a lateral *fasciculus cuneatus* (*column of Burdach*) and a medial *fasciculus gracilis* (*column of Goll*).

The various functional pathways, or fibre-tracts, within these funiculi cannot be distinguished in normal adult material, and have to be traced by experimental methods or by a study of development. The only exceptions to this statement in the case of the rat are the cortico-spinal tract and the tract of Lissauer, which are described below. Such analyses have not been made in the spinal cord of the rat, but as the general pattern appears to be essentially similar throughout the mammalia, a brief account of the pathways, based chiefly on the human subject, is included here. A diagram of the arrangement in the rabbit is also given in Fig. 2.

General Somatic Afferent System.

The peripheral receptive elements of this system fall into two groups, exteroceptors and proprioceptors, of which the first are stimulated by touch, pressure, heat, or cold, pain due to excessive stimulation also being included usually in this group, while the second transmit impulses arising in the muscles, joints, etc. Impulses of this character from any part of the animal except the head are carried to the spinal cord, where they are passed on to secondary fibres which are grouped according to the particular one of the above types of sensation which they subserve.

Upon entering the spinal cord, each somatic sensory fibre typically divides into two branches, which run up and down the cord respectively, the ascending branch being the longer. The fibres bearing pain and temperature impulses soon end

in the gray matter of the dorsal column. Of those bearing tactile impulses, some end very soon in the dorsal column, but others extend for a longer or shorter distance up the cord before terminating. Of the proprioceptive fibres, some end after a short course in the cord while others run right up to the lower end of the brain in company with some of the exteroceptive fibres, which give the discriminative character to sensibility (Head). All these primary fibres running along the spinal cord are grouped together in the dorsal funiculus, which is thus made up largely of ascending proprioceptive fibres mingled with some exteroceptive elements, a number of shorter exteroceptive fibres, both ascending and descending, and also certain axons which simply run from one part of the cord to another—longitudinal association fibres. At each level, the entering fibres take a position lateral to those ascending from behind. Hence the fasciculus gracilis contains the fibres which have come up from the more posterior part of the cord, the fasciculus cuneatus those which belong to the more anterior segments.

The cells of the dorsal column of the gray matter which receive impulses from these primary sensory fibres give rise to secondary axons, many of which pass across the middle line and take up a position in the lateral or ventral column of white matter on the opposite side, there ascending to the brain. These fibres are grouped in separate bundles according to the type of sensory impulse which they carry, and all the bundles together are known as the *spinal lemniscus*. Others of the secondary fibres enter the deeper part of the white matter in any of the three columns on the same side and pass up and down the cord for varying distances, finally ending in connection with the cells of the cord itself and thus serving as association paths. Yet other secondary axons arising in the dorsal column go into the ventral column to connect there with the motor cells giving rise to the ventral nerve roots. These fibres are thus part of short reflex paths pro-

ducing immediate responses at the same level as that where the stimulus is received.

Those proprioceptive fibres which do not ascend to the brain mostly end in connection with a group of cells near the base of the dorsal column known as *Clarke's column* (*nucleus dorsalis*), from which the secondary fibres pass to a superficial position on the same side, where they ascend as the dorsal and ventral spino-cerebellar tracts. This nucleus is not clearly defined in the rat.

The dorsal nerve root contains unmyelinated afferent fibres, of which the function is not known, but which may be somatic. These, upon entering the cord, take up a position superficial to the gelatinous substance of Rolando (Pl. V.), where, along with a number of endogenous fibres, they form a thin layer which may be detected in normal sections because the large preponderance of unmyelinated fibres makes it stain very lightly by the Weigert method and very deeply by silver methods. This is the *tract of Lissauer* (*fasciculus dorso-lateralis*). The fibres run a short distance up or down the cord and finally end in the gelatinous substance of Rolando. The greater part of the tract is located in the lateral funiculus in the rat, where there is an area just lateral to the gelatinous substance which has the same structure as the thin band superficial to the latter and which is continuous with it.

General Visceral Afferent System.

The peripheral fibres of this system convey from the visceral organs to the central nervous system impulses which do not ordinarily affect consciousness, but which make possible the nervous control of the functioning of these organs.

They enter the spinal cord through the dorsal nerve root along with the somatic afferent fibres and apparently end in the ventro-lateral portion of the dorsal column. The impulses may then be transmitted either to the visceral efferent

neurons of the cord or up to the brain, but the exact course of the fibres concerned in this has not yet been demonstrated.

Efferent Systems.

The efferent nerve fibres arise from cells situated in the ventral column of the gray matter. These cells are arranged in groups which correspond more or less to the areas of distribution of the fibres and which accordingly differ somewhat in different regions of the spinal cord. The visceral efferent cells form a group of small neurons situated laterally near the base of the ventral column in the thoracic region, this group being called the *intermedio-lateral cell column.* They lie in a projection of the gray matter into the white matter, which is named the *lateral column* and which is seen in the
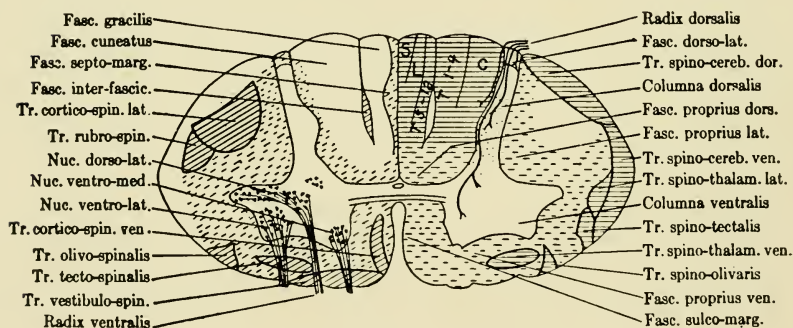
Fig. 1

Diagram of transverse section of fifth cervical segment of human spinal cord, from Herrick, Introduction to Neurology.

On the right side, the area occupied by the dorsal gray column (posterior horn) is stippled; on the left side, some of the groups of cells of the ventral gray column are indicated. In the white matter, the outlines of some of the more important tracts are schematically indicated, ascending fibres on the right side and descending fibres on the left. The same area of white matter is, in some cases, shaded on both sides of the figure. This indicates that ascending and descending fibres are mingled in these regions.

thoracic and upper cervical regions in man. In the rat cord examined by the writer, this projection was evident only in the last two cervical and the first thoracic segments (Pl. V.).
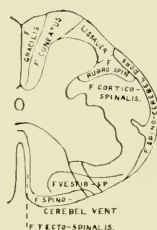
Fig 2.

Diagram of transverse section of the spinal cord of the rabbit, in the region of the cervical enlargement, after Winkler. According to v. Lenhossek and to Linowiecki, the cortico-spinal tract includes the area here assigned to the rubro-spinal tract and extends dorso-laterally to the surface of the cord. It will be observed that the location of the crossed cortico-spinal tract in the rabbit, unlike that in the rat, corresponds with that in man.

The efferent cells receive their stimuli chiefly, if not entirely, through correlation fibres which may come from neighbouring or distant parts of the cord or may descend from the brain. The most important descending tracts in the white matter are shown in the diagram (Fig. 1). The only one of these which can be observed in sections of the normal spinal cord of the rat is the *cortico-spinal or pyramidal tract (fasciculus cortico-spinalis cruciatus seu lateralis)*,[1] which stands out on account of the very poor myelination of its fibres. It may be seen forming the ventral or deep portion of the dorsal funiculus (Pl. V.), a position which differs entirely from that occupied by the same tract in man, where it lies in the dorsal part of the lateral funiculus. In man,

[1]The direct or ventral cortico-spinal tract of man does not appear to be represented in the rat (see p. 53).

moreover, its fibres are as well myelinated as are those sur-
rounding it, so that it is not distinguishable in sections of
normal material. The course of the cortico-spinal tract in
the brain will be described later.

CHAPTER IV.

MEDULLA OBLONGATA—GENERAL SOMATIC AFFERENT SYSTEM.

THE transition from the spinal cord to the medulla oblongata is gradual, the various parts changing their form and relations by degrees. The boundary is usually considered arbitrarily to be at the decussation of the pyramids. The greater part of the medulla oblongata contains the wide fourth ventricle and is known as the open portion, so that the section differs greatly in outline from sections of the spinal cord, being relatively broad and low (dorso-ventrally) with a hollow in the dorsal region representing the fourth ventricle. This concavity is lined with gray matter which corresponds to the central gray matter surrounding the canal of the spinal cord, and in which various special groups of cells appear. Extending right through the section in the median plane is a partition formed largely by decussating fibres, the *raphe*. Round the periphery of the section appear a number of more or less sharply marked off tracts and nuclei, such as the spinal V root and its nucleus, and between these and the raphe is a large area of intermingled gray and white matter known as the *substantia reticularis* or *reticular formation*. In a zone extending dorso-ventrally along each side of the raphe, the white fibres predominate, and hence this area is called the *substantia reticularis alba*, while the remainder of the formation, in which there is a larger proportion of gray matter, is the *substantia reticularis grisea* (Pl. VII.).

In the cranial nerves, three of the four primary functional types are represented by both general and special subdivisions, while the somatic motor group has special elements only,

making up seven out of the complete set of eight components. The general somatic afferent system is represented mainly in the trigeminal nerve, and a small number of fibres of this system occur in the facial,[1] glossopharyngeal, and vagus nerves. It is also present, in the form of proprioceptive fibres for muscle sense in the eye muscles, in the oculomotor, trochlear, and abducent nerves.

All the general somatic afferent fibres which carry exteroceptive impulses from the head region, no matter what their peripheral course may be, end centrally in a single nucleus of gray matter in the medulla oblongata. Since the great majority of such fibres are found in the trigeminal nerve, this centre has received the name of *trigeminal nucleus*. Upon entering the brain, most of the afferent fibres bifurcate, forming ascending and descending branches, of which the latter are the longer. A considerable number of unmyelinated and small myelinated fibres, however, have recently been found in the rat and other mammals to descend without bifurcating. They are believed to be pain fibres, as this sense is absent from the chief nucleus. The fibres are grouped together in a compact bundle running along the dorso-lateral aspect of the medulla in a superficial position. This *spinal V root (radix spinalis seu descendens trigemini)* extends downwards from the place of entry of the trigeminal nerve to the beginning of the spinal cord, where it becomes continuous with the tract of Lissauer (Pls. VI.-XI.). Some of the ascending branches of the sensory fibres pass upwards beyond the level of the entry of the fifth nerve before ending, forming an ascending extension of the bundle for a short distance. The number of fibres in this root and, consequently, the size of the fasciculus as a whole vary directly with the degree of development of general somatic sensibility in the head region.

[1]The presence of cutaneous sensory fibres in the facial nerve has been demonstrated in the mouse, and in various lower vertebrates. They probably occur in other mammals also.

In man, where such sensibility is not specially highly developed, the root is relatively small as compared with its size in the rat, which has great general sensibility in the snout region, particularly in connection with the vibrissae, or "whiskers".[1] In transverse sections, it appears as a large, crescentic area covering most of the lateral aspect of the medulla oblongata, in which position it may be followed from the beginning of the spinal cord up to the level of the fifth nerve. Traced up in this way, it will be seen to increase in size, being much smaller in the lower part of its course than in the upper. The obvious explanation of this fact is that all the fibres do not descend to the lower part of its course, a series of them leaving it all the way along to end in the adjacent gray matter.

The gray matter in which the afferent fibres of the general somatic system end is made up of two parts which are, however, continuous with each other. The first of these is the *chief sensory nucleus of the trigeminal nerve (nucleus principalis trigemini)*. It consists of a large mass of gray matter in the region of the entry of the nerve, lying in the lateral part of the medulla in close contact with the mass of sensory fibres (Pl. XI.), and extending anteriorly a short distance along with the ascending branches of these fibres, so as to receive their terminations. The trigeminal elements are covered superficially by other structures at this level, but a short distance posteriorly they emerge. Continuous with the chief nucleus is a column of gray matter situated immediately medial to the descending root and partly surrounded by it. This is the *spinal V nucleus (nucleus spinalis trigemini)*, which in the rat is as large as the chief nucleus in section, so that no precise line of demarcation can be drawn between them, though it is claimed that they differ in function (Pls.

[1]Meyersohn finds that, if cross sections at the level of the pyramidal decussation be magnified so as to make their diameters equal, the size of the spinal V root in the rat has the ratio to that in man of 1.21 : 0.25.

VII.-X.). In man, the chief nucleus appears as an enlarge-
ment at the anterior end of the column formed by the spinal
nucleus. Many fibres run through the nuclei, the lower part
of the spinal nucleus enclosing conspicuous bundles.

About the level of the anterior end of the hypoglossal
nucleus (p. 45) a small area of rather clear gray matter,
similar to the gelatinous substance of Rolando of the spinal
cord, appears superficial to the dorsal part of the spinal V
nucleus, and about the lower extremity of the fourth ventricle
this spreads out and forms a layer over the outer surface of
the nucleus, exactly as the gelatinous substance covers the
dorsal column in the cord (Pl. VII.). Traced downwards,
this is found to be continuous with the similar substance in
the cord, the nucleus as a whole being continuous with the
dorsal column. In connection with the cells of this nucleus,
the fibres of the spinal V root end, and from these cells arise
the secondary fibres which are to convey the impulse onwards.
Fasciculi concomitantes of the spinal V root lying in and
medial to the medial side of the spinal V nucleus, and largely
of heterolateral origin, are described for the rat by Fuse.

The secondary fibre-tracts arising from the chief sensory
and the spinal nuclei of the trigeminus cannot be followed in
normal material, coursing through the reticular substance
in a diffuse condition. They comprise both short reflex con-
nections, largely, if not entirely crossed, and ascending fibres
to the midbrain and to the thalamus (*trigeminal lemniscus*),
of which the majority are crossed. It would appear that the
fibres arising in the chief and spinal nuclei follow separate
routes, and that the trigeminal lemniscus arises only from
the chief nucleus. It comprises two portions, one in the
dorsal part of the reticular formation, the other, which
decussates slightly more posteriorly in the rat, running close
to the dorsal portion of the medial lemniscus and to the
raphe. Fuse states that in the rat the ventral trigeminal
lemniscus ends largely (he believes entirely) in the ventral

reticular nucleus of the tegmentum, from which, apparently, new fibres continue the pathway forward with the medial lemniscus to the thalamus.

Dorso-medial to the chief sensory V nucleus, lies a conspicuous group of large unipolar cells mingled with several small bundles of stout myelinated fibres. The cells give off similar fibres, which join those in the small bundles and run with them into the fifth nerve. Each fibre bifurcates, however, before passing out of the brain, one branch remaining within and ending either in the motor V nucleus or in a small group of cells dorso-medial to the sensory V nucleus. If the small bundles be now followed up the brain, they are found to be associated with a continually decreasing number of the unipolar cells, each of which gives rise to one of the fibres in the bundles, scattered along the lateral aspect of the central gray matter up to nearly the anterior end of the midbrain. These fibres form the *mesencephalic root of the trigeminus* (*radix mesencephalica trigemini*), the unipolar cells making up its nucleus (Pls. XI.-XIV.). They are sensory in function, probably concerned with muscle sensibility, the unipolar cells being apparently equivalent to peripheral ganglion cells which have developed within the brain instead of outside it. In fact some of the fibres of the mesencephalic root do arise from similar cells in the semilunar ganglion.

Degeneration experiments (Papez) reveal a group of descending fibres (*Tract of Probst*) rising apparently in the mesencephalic V root and running back in the rat dorsal to the chief sensory and the motor nuclei of the trigeminus. It continues posteriorly in the dorsal part of the reticular formation just ventro-medial to the solitary tract and its nuclei, and probably ends in relation to the salivatory nuclei.

Besides those somatic afferent fibres which enter through the cranial nerves, the medulla oblongata receives others which come up from the spinal cord. The fibres of the spinal lemniscus pass up from the white matter of the cord into the reticular formation of the medulla oblongata, whence they

continue upward through the midbrain to end finally in the
diencephalon. It is not possible to observe the course of
these fibres in the sections from normal material.

The dorsal funiculi of the cord are interrupted at the
lower end of the medulla oblongata. As one approaches
this region, passing up the spinal cord, the dorsal gray columns
are seen to spread apart somewhat, and a little below the decus-
sation of the pyramids, a small mass of gray matter appears
projecting dorsally from the central gray among the fibres of
the fasciculus cuneatus. This is the beginning of the *nucleus
cuneatus*. A little farther up than the lower end of the
pyramidal decussation, a broad median eminence also appears
on the dorsal surface of the central gray matter, the *nucleus
gracilis*. Still farther forward, another small part of the
nucleus gracilis is seen on each side among the fibres of its
fasciculus, and this becomes continuous with the projection
from the central gray matter. The latter, moreover, divides
into a small median nucleus and two lateral portions, con-
necting as just described with the groups of cells within the
white matter (Pl. VI.). The cuneate and gracile nuclei
increase rapidly in size, and as the fibres of the fasciculi end
within them, the latter are correspondingly reduced and
finally disappear. The cells of these *funicular nuclei* give
rise to secondary fibres which take a course ventrally and
medially in small groups, appearing in sections as *internal
arcuate fibres*. They cross the middle line, forming the
decussation of the lemniscus, and take up a position close to
the raphe (Pl. VII.). Here they form an ascending tract
which is known as the *medial lemniscus* (*lemniscus medialis,
medial fillet*), and which can be followed right through the
medulla oblongata in about the same position, though the
shape of its cross-section changes somewhat. It is a little
less conspicuous in the rat than in man. The details of form
of the gracile and cuneate nuclei in man also differ consider-
ably from those of the rat described above.

Special Somatic Afferent System.

THE special somatic afferent division comprises the auditory and vestibular elements and also the visual neurons. It really includes the olfactory neurons in addition to these, though the olfactory functions combine exteroceptive with interoceptive components, and it is usual to consider the olfactory structures with the visceral afferent group. Some authors object to this usage, however. Only the auditory and vestibular systems, which occur in the hindbrain, will be considered in the present chapter.

The fibres which convey auditory impulses to the brain form the cochlear branch of the eighth nerve, which branch ends in two large nuclei situated superficially on the dorso-lateral aspect of the medulla oblongata in its more anterior part. The *dorsal cochlear nucleus* (*nucleus cochlearis dorsalis*) or *tuberculum acusticum* extends from the dorsal part of the lateral surface round on to the dorsal surface, where it runs medially as far as the edge of the ventricle. It is situated immediately behind the attachment of the cerebellum to the medulla and its ventral end is produced forward along the lateral aspect of the cerebellar peduncles for some distance, where it is continuous with the flocculus. In the angle between the ventral extremity of this nucleus and the side of the oblongata lies another mass of gray matter of a more rounded shape, the *ventral cochlear nucleus* (*nucleus cochlearis ventralis*). This does not extend so far posteriorly as the tuberculum acusticum, but reaches considerably farther

forward.[1]   It is quite distinct from the latter nucleus in sections owing to the arrangement of the nerve-fibres, and the character of the cells in the two centres differs (Pls. III., IX.-XI.).

Some of the secondary fibres from the dorsal nucleus pass ventrally along the medial aspect of the ventral nucleus, where they join those arising in the latter.   These fibres form a large tract which passes ventrally and a little anteriorly over the surface of the medulla until it gets near the median line, where many of the fibres become deeper in position, breaking up into smaller fascicles and leaving only a thin layer superficial to the pyramids.   They decussate and pass towards the lateral part of the other side of the oblongata in a somewhat more diffuse condition than in the earlier part of their course.   Up to this point the tract is known as the *trapezoid body* (*corpus trapezoides*), but it now changes its direction, running anteriorly, and is given a new name, the *lateral lemniscus* (*lemniscus lateralis, lateral fillet*) (Pls. II., IX.-XIV.).   In the human brain the trapezoid body is completely covered superficially by the greatly enlarged pons.

The other secondary fibres arising in the dorsal cochlear nucleus pass medially (*striae medullares acusticae*), dipping some distance below the floor of the fourth ventricle in the form of small scattered groups of arcuate fibres.   About two-thirds of these decussate (*decussation of v. Monakow*) and, running forward dorsal to the superior olive, join the lateral lemniscus.

[1]There may be distinguished in the ventral cochlear nucleus: dorso-medial, ventro-medial, dorso-lateral, central cell groups, and in the dorsal cochlear nucleus: superficial, middle, and deep layers may be observed.

The difference in the level of the two nuclei is greater in man, where they do not overlap, the dorsal nucleus having been pushed back by the enlargement of the restiform body and the ventral nucleus having become imbedded in the side of the brachium pontis.   Also, the dorsal nucleus is relatively smaller and the ventral nucleus is relatively larger in the human brain.

The trapezoid body comes into relation with certain masses of gray matter in the transverse part of its course, of which the most conspicuous are the *superior olivary nuclei*. These are more largely developed in the rat than in man—as are also the cochlear nuclei—and have the form in this and many other mammals of a lamina folded twice, so as to appear S-shaped in cross section. Immediately medial to each is a smaller lamina, the *accessory superior olivary nucleus*, and some little distance medial to this again is a much less definitely circumscribed group of cells, the *nucleus of the trapezoid body*. Some of the trapezoid fibres end in some one of these nuclei, either before or after crossing the median plane, and fibres arising from them pass into the lateral lemniscus. Many of the fibres arising in the superior olivary nucleus, however, run in a rather diffuse tract which may be seen passing dorso-medially towards a small group of cells near the floor of the ventricle, the nucleus of the sixth nerve[1] (Pl. X.). These fibres mediate direct reflex movements of the eyes in response to auditory stimuli. Other such fibres run through the reticular substance from all the nuclei of this group to form short reflex paths to other motor nuclei.

The superior olivary complex of the rat, which has been analyzed as follows by Fuse, contains more different elements than are enumerated above. Besides the principal superior olivary nucleus, there are (1) the accessory superior olivary nucleus, consisting of a small, dorso-ventrally elongated gray mass and a largely-developed dorso-medial accessory group of cells; (2) the nucleus of the trapezoid body; (3) the nucleus praeolivaris internus; (4) the dorsal accessory nucleus of the principal superior olive; and (5) the nucleus praeolivaris externus (poorly developed in the rat).

The accessory superior olivary nucleus receives trapezoid fibres (mostly heterolateral) and gives off axòns to the medial lemniscus and to the homolateral nucleus of the trapezoid body. It also has connections with its own medio-dorsal accessory cell-group, and with the nucleus praeolivaris internus of the same side. The medio-dorsal cell-group is larger than the rest of the nucleus, and is separated from the nucleus of

[1]Fuse doubts whether they reach the abducens nucleus in the rat.

the trapezoid body by thick bundles of trapezoid fibres. Its connections are similar to those of the other part of the nucleus.

The nucleus of the trapezoid body lies medio-ventral to the last-mentioned group and is differentiated from the more ventro-laterally placed nucleus praeolivaris internus by its larger cells. It is traversed by many longitudinal fibre bundles. There are extensive fibre connections with the lateral parts of the medial lemniscus and the pyramidal tract as well as with the accessory superior olivary nucleus, but none with the lateral lemniscus of the same side. There are considerable heterolateral connections also.

The nucleus praeolivaris internus receives fibres of the corpus trapezoides, mostly of heterolateral origin. The lateral part of the nucleus sends most of its axons across the raphe, while most of those from the medial part enter the homolateral medial lemniscus and pyramidal tract.

The dorsal accessory nucleus of the principal superior olive lies over the dorsal hilus of the latter in relation to the fibres of v. Monakow.

The trapezoid fibres ending in the principal superior olivary nucleus are partly hetero- but chiefly homolateral in origin and only about one-quarter to one-third of the fibres coming directly from the cochlear nuclei decussate. These apparently originate chiefly in the ventral cochlear nucleus. The crossed fibres of the trapezoid body originating in the nucleus of the trapezoid body, superior accessory olivary nucleus, nucleus praeolivaris internus, ventral cochlear nucleus, dorsal cochlear nucleus and chief superior olivary nucleus are of decreasing numerical importance in the order named, and are accompanied by a few fibres from the spinal V nucleus and from the reticular formation. Most of these fibres are distributed more caudally after decussating, while most of those from the cochlear nucleus end in the olivary complex. Apart from the fibres of v. Monakow, the lateral lemniscus is very largely of homolateral origin.

The lateral lemniscus passes directly forwards into the midbrain, where many of its fibres may be followed into the posterior colliculus (p. 68). Others pass on with the fibres arising in that region to the medial geniculate body (p. 79). In the lower part of its course, the fibres of the lateral lemniscus enclose a group of cells, the *ventral nucleus of the lateral lemniscus (nucleus ventralis lemnisci lateralis)*, in connection with which a number of them end. The lemniscus then follows a somewhat antero-dorsal course and breaks up into small fibre-bundles as it approaches the midbrain. Between

the bundles is a large amount of grey matter, constituting the *dorsal nucleus of the lateral lemniscus (nucleus dorsalis lemnisci lateralis)*. Behind this point its fibres are not very easily distinguished from those of the ventral spino-cerebellar tract (p. 52), which have a similar arrangement and general direction, and which lie immediately lateral and dorsal to the lemniscus.

The vestibular nerve, which conveys proprioceptive impulses, chiefly of an equilibratory nature, ends in relation with a somewhat extensive group of nuclei placed dorso-laterally. These consist of a more or less continuous column of gray matter which is rather clearly divisible into parts. At the level of entry of the root is a large-celled mass in a lateral position close to the ventricle, the *lateral vestibular nucleus*[1] *(nucleus lateralis nervi vestibuli)* or *nucleus of Deiters* (Pls. IX. X.). Extending posteriorly from this, just as the spinal V nucleus extends posteriorly from the chief sensory V nucleus, is the *descending vestibular nucleus (nucleus descendens nervi vestibuli seu octavi)*, which is accompanied by bundles of the root fibres, the *descending vestibular root* (Pl. VIII.). This root can be traced down as far as the beginning of the spinal cord, where it ends in connection with a small nucleus lying between the cuneate nucleus and the gelatinous substance.

There are also ascending branches of the root fibres forming an ascending root, as in the case of nerve V, each fibre bifurcating on entering the brain. Many of these ascending branches end in an anterior nucleus, the *nucleus of Bechterew* or *superior vestibular nucleus*, which extends from the nucleus of Deiters antero-dorsally, projecting into the cerebellar peduncles (Pl. X.).

Medial to the nucleus of Deiters and the descending

[1]Fuse distinguishes seven parts in this nucleus in the rat and other rodents: dorso-lateral, dorsal, middle or central, dorso-medial, ventro-medial, intravestibular, and triangularis portions. He also finds two or three cell groups in the nucleus of Bechterew.

nucleus, and immediately under the floor of the fourth
ventricle, lies a small-celled nucleus of roughly triangular form
in cross section, the *chief vestibular nucleus* (*dorsal vestibular
nucleus, nucleus dorsalis seu medialis nervi vestibuli, nucleus
triangularis*).[1] This large nucleus extends all the way from
a point a little behind the entrance of the V nerve root to
the level of the anterior part of the hypoglossal nucleus
(Pls. VIII.-X.).

Some of the ascending vestibular fibres do not end in
any of these nuclei but run directly into the cerebellum,
where they end in the roof nuclei and in certain parts of the
cortex (Pl. X.).

Fortuyn also saw vestibular fibres entering the ventral
cochlear nucleus in the rat.

Secondary fibres from the nuclei of Deiters and Bechterew
join the direct fibres to the cerebellum and end with them in
that structure.

Other fibres arising in these nuclei pass medially to enter
an important longitudinal correlation tract on either the same
or the opposite side (Pl. X.). This tract is the medial longi-
tudinal bundle, which lies in the angle between the raphe
and the gray matter of the ventricular floor. Through this
tract, the vestibular impulses are conveyed to various motor
centres, particularly the eye-muscle nuclei, the *ascending tract
of Deiters* (*tractus Deiters ascendens*) forming a definite group
of fibres in the lateral part of the bundle in the midbrain.

Yet other fibres from Deiters' nucleus form a diffuse tract
in the reticular formation, which runs down to the spinal
cord, conveying impulses to the spinal motor neurons. This
is the *vestibulo-spinal tract* (*fasciculus vestibulo-spinalis, tractus
Deiters descendens*). Its fibres pass obliquely between the

[1] The term *triangular nucleus* has also been applied to the cuneate
nucleus.

The chief vestibular nucleus contains several centres and receives
vestibular fibres only in its lateral part (Fuse).

more lateral fascicles of the ascending limb of the facial root, and appear to be partly of heterolateral origin.

The fibres arising in the chief vestibular nucleus cross to the opposite side, where they course through the reticular formation to make various reflex connections.   Fuse states that many of these fibres are uncrossed in the rat.

The complexity of the cochlear and vestibular systems is probably considerably greater than is indicated by the foregoing account, as has been shown by Winkler to be the case in the rabbit.

CHAPTER VI.

Visceral Afferent System.

THE visceral afferent system, like the somatic, is represented in the cranial nerves by both general and special subdivisions, of which the latter is concerned with the sense of taste. Smell may also be included in this category on physiological grounds, but its structural representatives are independent, whatever their phylogenetic origin may have been. Both these components are represented in each of the tenth, ninth and seventh nerves. Unlike the somatic system, the two subdivisions of the visceral afferent group end in the same column of gray matter according to the account usually given.

The sensory fibres of the glossopharyngeal and vagus nerves upon entering the substance of the brain run in small fascicles to a position between the dorsal end of the spinal V nucleus and the ventro-lateral angle of the chief vestibular nucleus. Here they take up a longitudinal, descending direction, forming the *fasciculus solitarius*, which runs down to the beginning of the spinal cord (Pls. VI.-IX.). The afferent facial fibres, which enter the brain farther forward, also run back and slightly mediad near the dorsal edge of the spinal V root and join the descending fibres of nerve IX. The fasciculus is accompanied by two columns of gray matter, of which the large one medial to it is the *nucleus of the fasciculus solitarius (nucleus fasciculi solitarii)*, while the one which lies ventro-lateral to it is the *nucleus parasolitarius*. The former of these has a very clear appearance and is a conspicuous object in sections. Its anterior end is covered dorsally by the chief vestibular nucleus, but it soon emerges and occupies a position

medial to this and directly under the floor of the fourth ventricle. Some of the fibres of the fasciculus solitarius end in these nuclei,[1] but many of them descend to about the level of the decussation of the pyramids, where they decussate in a mass of gray matter dorsal to the central canal and continuous with the nuclei of the fasciculi solitarii of the two sides. This mass is the *commissural nucleus of Cajal* (*nucleus commissuralis*, Pl. VI.), in which the fibres terminate after decussating within it, forming the *commissura infima*. The commissura infima is not ordinarily seen in Weigert preparations as it contains very few myelinated fibres. A few of the fibres do not decussate, but run right into the upper part of the spinal cord on the same side.

While the fasciculus solitarius and its gray matter are usually considered to contain both the general visceral and the gustatory connections, there is some evidence in favour of the view that only the former components end in this way. According to the supporters of this interpretation, a considerable proportion of the visceral afferent fibres, at least from nerves IX and X, do not end in the centres mentioned, and chiefly on comparative grounds, these are believed to be the gustatory elements. The nuclei with which they come into relation are two in number on each side, and lie at the level of the entering nerve roots. The larger and more distinct is a small-celled nucleus which is wedged in between the anterior end of the hypoglossal nucleus and the dorsal motor vagus nucleus (p. 47), and is named the *nucleus intercalatus of Staderini* (Pl. VIII.). This nucleus extends medially, forming a cap over the anterior extremity of the hypoglossal nucleus, and becoming continuous with a small mass next to the median line, the *nucleus funiculi teretis*. In front of the hypoglossal nucleus, it enlarges and occupies the position of the latter for a short distance. It also connects laterally, dorsal to the motor X nucleus, with the second centre to which gustatory functions are attributed, viz., a small mass which forms the ventro-medial angle of the chief vestibular nucleus, and which has usually been considered as part of that centre. Allen, however, could trace no visceral afferent fibres to either of these centres in the guinea pig, but found them all to enter the fasciculus solitarius.

[1]Allen found no terminals from the tractus solitarius in the nucleus parasolitarius of the guinea pig (Jour. Comp. Neur., vol. 35).

The secondary visceral pathways are not well known. They include descending fibres to the cervical spinal cord, concerned probably with respiratory reflexes and reflexes of the digestive organs, such as vomiting, and an ascending path probably to the hypothalamus. Allen, however, has demonstrated in the guinea pig that the ascending secondary fibres, unless they are unmyelated, must run with the medial lemniscus of the opposite side to the thalamus.

CHAPTER VII.

The Motor System.

Somatic Efferent Column.

ALL the somatic muscles (those derived from the myo-
tomes of the embryo) controlled by cranial nerves
are of a rather highly specialized character and their
nerve elements are consequently classified as special somatic
efferent, the general somatic efferent component being con-
fined to the spinal nerves. These special motor fibres are
found in the third, fourth, and sixth nerves, where they
control movements of the eyeball, and in the twelfth nerve,
where they regulate the movements of the musculature of the
tongue.

The nuclei of these nerves are arranged in a linear series,
being parts of a single somatic efferent column which has
become broken into separate centres corresponding to the
nerves through which its fibres run. The oculomotor and
trochlear nuclei lie in the midbrain but the abducent and
hypoglossal centres are in the medulla oblongata.

The position of the column corresponds primitively to
that of the ventral gray column in the spinal cord, of which
it is to be considered an anterior continuation. The location
of the cells, however, has undergone a change, there having
been a migration towards the most important source of
stimulation. In the case of the *hypoglossal nucleus* (XII),
the majority of stimuli are received, probably, from the
visceral afferent nuclei, and the nucleus has moved antero-
dorsally and taken up a position near the floor of the ventricle,
close to these centres (Pls. VI.-VIII.). Here it appears as a
slender, elongated mass of gray matter extending from the

level of the decussation of the pyramids to a point some little distance forward under the floor of the fourth ventricle. Several different groups of cells, which are related to special muscles or sets of muscles, are distinguishable in the nucleus. The hypoglossal root fibres are arranged in small bundles which pass directly ventrally and a little laterally to emerge at the outer edge of the pyramid (pp. 12, 53).

The *nucleus abducens* (VI) lies considerably farther forward, having migrated from a position between the levels of the nuclei VII and IX to one in front of the nucleus VII. This change probably took place largely under the influence of fibres from the anterior parts of the medial and lateral vestibular nuclei running chiefly in the medial longitudinal bundle. Having reached this more anterior position, it has farther moved dorso-laterally in many mammals, so as to lie still nearer these centres. This is the condition seen in man, where the nucleus VI lies near the floor of the fourth ventricle and lateral to the genu of the VII nerve root (p. 48), as it does also in the rabbit. In the rat, however, the nucleus has not undergone the lateral movement, but appears as a small, rather scattered group of cells wedged in between the genu of the VII root and the medial longitudinal fasciculus and extending a short distance ventrally along the side of the latter (Pl. X.). Its root fibres pass out directly in a course exactly parallel to that of the XII root fibres farther back.

Visceral Efferent Nuclei.

The visceral efferent centres, like the somatic, may be considered to be an anterior continuation of the corresponding column in the spinal cord. They have become divided into separate general and special columns, however, and the changes of location undergone by the individual nuclei are more diverse than are those of the somatic centres.

General visceral efferent fibres occur in the roots of nerves III, VII, IX, X, and XI, whence they run into

sympathetic ganglia. Those of the X and XI nerves arise in a single column of cells which has a dorsal situation near the floor of the fourth ventricle (Pls. VI.-VIII.). This nucleus —the *dorsal motor vagus nucleus* (*nucleus motorius dorsalis X*) —ends anteriorly a short distance in front of the rostral extremity of the nucleus XII, where it is separated from the fourth ventricle by the large nucleus of Staderini and the chief vestibular nucleus and lies just medial to the corresponding sensory centre (nucleus fasciculi solitarii). Passing backwards, the nucleus of Staderini rapidly decreases until the vagus nucleus, which grows somewhat larger, comes to lie lateral to it and immediately under the floor of the ventricle. From here, it can be traced down into the closed part of the oblongata, where it ends near the posterior extremity of the hypoglossal nucleus.

The general visceral components of the facial and the glossopharyngeal nerves are connected with the salivary glands, and their nuclei are the *superior* and the *inferior salivatory nuclei* respectively. These are small groups of scattered cells. They are practically continuous with each other and occupy a more lateral and deeper position than the dorsal motor X nucleus, a short distance in front of its anterior extremity.

The special visceral efferent cells, on the other hand, which send fibres into nerves V, VII, IX, X, and XI, have undergone a marked change in position in a ventral and somewhat lateral direction, a change which has gone farthest in the case of the *motor facial nucleus* (*nucleus motorius VII*). This large group of cells is to be found close to the ventral surface of the brain, midway between the spinal V root and the pyramid, and some distance behind the level where its root emerges (Pl. IX.). It is composed of several separate cell-masses, which Papez has found in both rat and cat to give rise to the fibres of distinct branches of the nerve. The root fibres do not run directly to the point of emergence, but

pass in a dorso-medial direction towards the position whence the cells have migrated. Close to the floor of the ventricle, they turn forwards and group themselves into a compact bundle, the *genu* or *ascending portion of the motor VII root*. After ascending a short distance to a point just in front of the nucleus VI, the root turns sharply at about a right angle and runs ventro-laterally to emerge at the ventral edge of the spinal V root (Pls. X., XI.). In the human brain, the facial nucleus is relatively rather smaller than in the rat, and is not quite so far ventral in position, while its rostral end lies dorso-lateral to the superior olive instead of practically directly behind it, as in the rat. This is probably due partly to the more dorsal position in man of the reduced spinal V nucleus, from which the motor VII nucleus receives impulses, and partly to the enormous development of the pons. The latter factor has pushed back the emerging motor VII root in man until it lies beside the front part of its nucleus, ventral to which the posterior portion of the pons itself extends.

The special motor cells of the IX and X nerves form a continuous column of very much smaller size than the motor facial nucleus. This is the *nucleus ambiguus*, which is found in a position similar to that of the motor VII nucleus, but not so near the surface, being medial to the ventral edge of the spinal V nucleus (Pl. VIII.). Its anterior extremity is about on a level with that of the dorsal motor X nucleus, but posteriorly it gradually thins out until it is represented by a few isolated cells so irregularly scattered that its posterior end cannot be exactly determined.

The root fibres from this nucleus run dorso-medially and join those from the dorsal nucleus, passing out with them in small groups in a lateral direction.

The special motor fibres of the XI nerve arise from the *nucleus accessorius*, which may be regarded also as part of the visceral motor column which has changed its position, migrating in a postero-lateral direction and being joined by

visceral motor cells of those segments of the spinal cord in which it lies (Pl. VI.). It extends from near the level of the posterior end of the hypoglossal nucleus through the upper cervical segments of the cord.

There remains to be considered one other special visceral efferent centre, namely the *motor trigeminal nucleus* (*nucleus motorius V, nucleus masticatorius*), which controls the movements of the jaw muscles. This nucleus consists of a rather conspicuous group of large cells which do not lie very close together. It is situated medially to the chief sensory V nucleus and gives rise to the motor fibres of the V nerve (Pl. XI.). These form large fascicles which may be observed passing out in an antero-ventral and somewhat lateral direction.

The various changes in position which we have just seen to have taken place in the development (both ontogenetic and phylogenetic) of the motor nuclei are prominent examples of a principle which seems to be active throughout the nervous system, and which has been called by Kappers *neurobiotaxis*. The most essential part of this principle may be summed up by saying that two nerve cells which are simultaneously or consecutively excited exert an attractive influence on each other, as a result of which the cell body tends to migrate during development towards any other neuron from which it receives stimuli.

CHAPTER VIII.

Correlation Centres and Tracts in the Medulla Oblongata and Pons.

THE nerve centres and pathways which have been considered so far do not by any means exhaust the list of structures visible in sections of the medulla oblongata and pons. There are pathways leading to and from both the cerebellum and the higher regions of the brain, and there are structures which serve for correlation of impulses within this region itself. The functional difference between the correlation centres and the sensory nuclei is, however, one of degree rather than of kind, for sensory nuclei usually receive stimuli from several different sources, as do correlation nuclei. The only real difference is that the sensory centre receives a great majority of its stimuli from one source, frequently outside the body.

One of the most conspicuous correlation centres in the brain stem is a prominent mass of gray matter lying in a ventro-medial situation and having a very characteristic appearance in section (Pls. VII., VIII., XXVI.). This is the inferior olivary complex, of which the functional relations are still very imperfectly understood, but which is known to be intimately related with the cerebellum. The mass is divisible into three distinct nuclei, the *medial olive* (*medial accessory olivary nucleus*), the *dorsal olive* (*dorsal accessory olivary nucleus*), and the *ventro-lateral* or *principal olive* (*inferior olivary nucleus, oliva inferior*), which are continuous with each other at certain points. Each of these is an elongated lamella of rather irregular outline, so that its exact form and position vary at different levels. The medial nucleus extends

considerably farther posteriorly than do the other two, which are nearly co-extensive. The principal nucleus differs from the others in being folded lengthwise so as to form a sort of pocket with an opening, the *hilus*, directed medially. Thus a section through the middle part of the nucleus is U-shaped, but as the pocket is somewhat narrowed round the opening, this form does not appear in sections near either end of the nucleus. In higher mammals, including man, the accessory nuclei are similar to those of the rat, but the principal nucleus is very greatly enlarged and folded, though still retaining the pocket-like form.

Streaming through the hilus and round and through the nuclei are many fibres which are chiefly efferent axons from the olives to the cerebellum. They cross directly to the other side and curve up to the restiform body (vide infra), with which they become incorporated.

Other correlation centres are present in the form of large and medium-sized cells scattered through the reticular formation. These are the reticular nuclei,[1] which receive impulses from various sources and transmit the resultant impulses directly to motor centres (Pls. VII., VIII.).

The *nucleus of Roller*, which lies just ventral to the hypoglossal nucleus and has sometimes been supposed to be related to it, belongs to this group. In another nucleus of the group, the *ventral reticular nucleus of the tegmentum (nucleus reticularis tegmenti ventralis)*, which extends forward from the level of the oral end of the superior olive in a medial position, Fuse believes that the trigeminal lemniscus and many of the more dorsal fibres of the medial lemniscus are interrupted in the rat. He finds that this group is composed of large cells, of which the axons are largely uncrossed, and medium-sized and small cells of which the axons are mostly crossed (especially the more posterior ones), and that it receives many arcuate fibres from the ventro-lateral part of the reticular formation of the same side.

[1] For a description of these nuclei in the rabbit, see Pekelský, 1922. This author examined also Mus rattus, where he found no important difference in respect of these nuclei.

Fuse has described in some detail for the rat and other types *caudal and oral ventro-medial cell groups of the spinal V root* lying between the latter and the superior olive, and a few small cell groups ventral to the motor V nucleus (Pls. IX., XI.).

The medulla oblongata is furthermore traversed by numerous pathways connecting higher and lower regions of the brain. Some of these—the secondary sensory tracts— have already been considered. Among the ascending pathways, there are to be noted in addition to these the *restiform body (corpus restiforme)* or *inferior cerebellar peduncle* and the *ventral spino-cerebellar tract* which forms a large part of the composite *tract of Gowers*. The former is the direct continuation of the dorsal spino-cerebellar tract of the spinal cord, to which are added various elements originating in the medulla oblongata. It forms a conspicuous, compact bundle in the dorso-lateral corner of the sections (oval area), where it can be followed up into the cerebellum (Pls. IX.-XI.). The ventral spino-cerebellar tract lies superficially in the ventro-lateral region, where it is not clearly marked off from the surrounding tissue (Pl. VIII.). In the upper part of the oblongata, anterior to the trigeminal nuclei, it may be seen to turn dorsally and pass to a position dorsal to the brachium conjunctivum (vide infra), with which it then runs back into the cerebellum (Pl. XI.). As it passes dorsally, it appears in the form of numerous small bundles which may easily be confused with the lateral lemniscus, as this tract runs in a similar direction immediately medial to it.

There may also be included in this group the *brachium conjunctivum*, or *superior cerebellar peduncle*, which traverses the uppermost part of the hindbrain in passing from the cerebellum into the midbrain. It is a rather large bundle situated laterally, at each side of the ventricle, and having a dorso-ventrally flattened form. It passes in an antero-ventral direction into the midbrain, becoming decreasingly compact as it does so (Pls. XI., XII.).

Containing both ascending and descending correlation fibres, is the *medial longitudinal bundle* (*fasciculus longitudinalis medialis, dorsalis, seu posterior*), a rather distinct bundle lying close to the central gray matter immediately on each side of the raphe, and containing many different kinds of fibres (Pls. VII.-XV.).

The most conspicuous descending tract is the *pyramidal tract*, which runs directly posteriorly in a ventral position, carrying motor impulses to the somatic muscles. As it enters the region of the pons from the midbrain, this tract is accompanied by numerous cortico-pontine fibres which end in the nucleus pontis (infra), thus decreasing considerably the size of the bundle as a whole. It is also accompanied by cortico-bulbar fibres, which pass to the motor nuclei of the medulla oblongata. The remainder of the tract[1] (cortico-spinal or pyramidal tract), when it reaches the lower end of the oblongata, decussates in the form of numerous rather large bundles—the *pyramidal decussation* (Pl. VI.)—and runs dorsally to take up a position in the ventral part of the dorsal funiculus of the spinal cord, where it has already been observed.

In man and some other mammals, the decussation is incomplete, a small proportion of the fibres continuing straight down into the ventral funiculus of the same side and crossing over singly just before ending in the ventral gray matter. In the rat, however, the decussation appears to be complete or practically so.

Related functionally with the pyramidal tract is the *rubrospinal tract* (*fasciculus rubro-spinalis*), which conveys impulses

[1]Bregmann finds that the area of cross section of the cortico-spinal tract just before it decussates is 5.3% of the area of the section of the spinal cord just behind the decussation in the rat. The corresponding ratio for man is 30.0%. These figures do not represent the relative number of fibres, however, since they do not consider the relative sizes of the individual axons, a factor which is complicated by the great difference in myelination.

to influence the tone of the body muscles. This bundle runs
through the reticular formation, where it is not distinct from
its surroundings. As it enters the region of the pons from
above, the rubro-spinal tract lies just medial to the lateral
lemniscus. Upon reaching the level of the trigeminal nuclei,
it takes up a more superficial position immediately ventral
to the spinal V nucleus and root, separating the latter from
the ventral spino-cerebellar tract, and in this position it
descends directly into the spinal cord (Pls. X., XIII.).

Ventral to the medial longitudinal fasciculus is situated a
bundle of fibres, somewhat diffuse in the rat, rising in the
anterior colliculi of the midbrain and descending to the spinal
cord, where degeneration experiments in the rat reveal it
as an extensive zone of finely scattered fibres external to the
fasciculus proprius in the ventral funiculus. This is the
tecto-spinal tract (*fasciculus tecto-spinalis seu praedorsalis*)
(Pls. VII.-XIII.).

The reticular formation, of course, contains many other
pathways, which, however, are mostly diffuse in arrangement
and cannot be observed in sections of normal material.

Finally, there may be mentioned here the *pons* (*pons
Varolii*) (Pls. II., XII., XIII., XXVI.). This is a large mass
of transverse fibres running round the ventral surface of the
anterior part of the medulla oblongata and turning dorsally
at each side to pass up into the cerebellum as the *brachium
pontis* or *middle cerebellar peduncle* (Pls. III., XII.). In the
ventral part of their course, the fibres spread apart to allow
the cerebral peduncles (pyramidal tracts+cortico-bulbar
and -pontine tracts) to descend between them and also to
surround a considerable amount of gray matter, the *pontine
nuclei*. These nuclei receive impulses from various sources,
particularly from the cerebral cortex[1] through the cortico-
pontine tracts, and give rise to the fibres of the pons itself.

[1]Frontal and temporal lobes in man. The former, however, is
exceedingly rudimentary in the rat.

The latter usually decussate and convey their impulses up to the cerebellar hemisphere on the opposite side. The pons is to be regarded as a structure which has been added to the primitive hindbrain coincident with the development of the cerebellar hemispheres, for the purpose, primarily, of putting these into communication with the cerebral cortex. Hence it is very much smaller in the rat than in man, where both the cerebral cortex and the cerebellar hemispheres are much more largely developed.

CHAPTER IX.

The Cerebellum.

TRANSVERSE sections through the cerebellum show the various lobules which cross the median plane, the *lobus ansiformis* or *cerebellar hemisphere* on each side, and the floccular lobe projecting laterally below it. These parts have already been described in the first chapter. Those lobules which are medially situated are best seen in a sagittal section (Fig. 3). Such a section also shows the branching arrangement of the white matter which has received the name of *arbor vitae*, in which each little branch is one of the transversely disposed lamellae cut across.
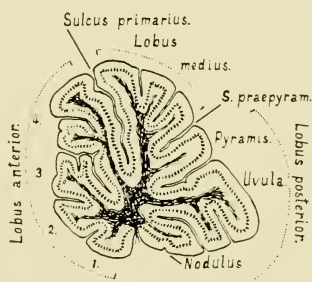
Fig. 3

Median sagittal section of the cerebellum of the rat.

In general, the sections of the cerebellum show it to consist of a large mass of white matter, the *medulla of the cerebellum*, over which is disposed a greatly folded layer of gray matter, the *cerebellar cortex*. The cortex has a very complex structure, being made up of many different kinds of

neurons, but in ordinary sections it appears to be composed of only two distinct layers. The outer, or *molecular layer*, is of a homogeneous or very finely punctate appearance, with a few small cell-nuclei scattered through it. The inner, or *granular layer*, on the other hand, is composed of cell-bodies closely packed together. The outermost row of cells in this layer is made up of very characteristic large, pyriform cells, the *Purkinje cells*, of which the axons pass straight down into the white matter, while the large, branched dendrites extend out through the molecular layer. The dendrites of each Purkinje cell spread out in a single plane sagittally placed, *i.e.*, at right angles to the axis of the cerebellar lamella. Each dendrite is thus in a position to receive a maximum number of stimuli from the numerous, fine fibres in the molecular layer which run lengthwise of the lamella.

The gray matter of the cerebellum, however, is not all superficial in position. There are also certain masses imbedded in the deeper part of the white matter, near the roof of the fourth ventricle (Pl. IX.). Four pairs of these nuclei are recognized, named in a medio-lateral direction respectively *nucleus fastigii* (*nucleus tecti*), *nucleus globosus*, *nucleus emboliformis*, and *nucleus dentatus* (*dentate nucleus* or *cerebellar olive*). The dentate nucleus is a little larger than the other nuclei and stretches out into the base of the stalk of the floccular lobe. It is the ending-place of many of the axons of the Purkinje cells, and the place of origin of most of the fibres in the brachium conjunctivum. In the rat, this nucleus is a compact mass slightly hollowed medially, so that it appears somewhat curved in section. In man, the hollowing has increased and the nucleus has grown as a whole until it appears as a much-folded, pouch-shaped lamella, very similar in form to the inferior olivary nucleus. This increase in size of the dentate nucleus is apparently correlated with the larger development of the cerebellar hemisphere. The three remaining nuclei are proportionately larger in the rat than

in man and are more or less fused with each other (particularly the nuclei globosus and emboliformis, which are often together called *nucleus intermedius* or *interpositus* in lower mammals) in most sections. They receive fibres from the Purkinje cells, and the nucleus fastigii, which is related particularly to the vestibular apparatus, also receives nerve endings from other parts of the nervous system. The axons of the nuclei globosus and emboliformis join those of the dentate nucleus in the brachium conjunctivum, while those of the nucleus fastigii pass to the reticular formation of the hind brain as the *cerebello-bulbar* or *fastigio-bulbar tracts*. Some of these fibres to the hindbrain form a rather definite bundle, the *tractus arcuatus Russell*, or *fasciculus cerebello-bulbaris* (*fasciculus uncinatus*) (Pl. XI.). This leaves the ventral surfaces of the deep nuclei and curves anteriorly and laterally round the dorsal aspect of the brachium conjunctivum, between it and the ventral spino-cerebellar tract. It then runs postero-ventro-laterally, medial to the restiform body, and joins the descending vestibular root, with which it passes backwards.

CHAPTER X.

The Midbrain.

THE general form of the midbrain, or mesencephalon, is less modified from the early embryonic condition than is that of either of the other primary subdivisions of the brain. It retains the condition of a thick-walled tube connecting the forebrain and the hindbrain with only a little modification of the shape of the walls by a greater thickening ventrally than dorsally, and by the moulding of the dorsal wall, or *tectum*, into four eminences, the *corpora quadrigemina* (Pls. III., XII.-XVI.). The narrow ventricle is variously known as the *cerebral aqueduct*, the *aqueduct of Sylvius*, or the *iter*. The thick wall ventral to the aqueduct is the *cerebral peduncles*, which are divided into a thick *tegmentum*, in the deep position, and a pair of large flattened bands of longitudinal fibres situated superficially, the *basis pedunculi* or *pes pedunculi*. Tegmentum and basis are separated by a layer of gray matter, the *substantia nigra* (Pls. XIII.-XVI.).

Dorsal to the substantia nigra, the tegmentum consists of reticular formation continuous with that of the medulla oblongata, while dorsal to this again is a rather thick layer of central gray matter. Into the tegmentum may be traced many of the longitudinal tracts which have been observed in the corresponding region of the hindbrain. In the posterior part, the fibres of the lateral lemniscus are to be seen at each side surrounding their dorsal nucleus and running antero-dorsally into the tectum. From the enlarged anterior end of the dorsal nucleus of the lateral lemniscus, arises a thin bundle of transverse fibres, the *commissure of the lateral lemniscus* or *commissure of Probst* (Pl. XII.). After decussating, these

fibres run into the corresponding nucleus of the other side and curve dorsally in the lemniscus to end in the posterior colliculus (Papez).

Ventrally, the medial lemniscus continues forward in the same position which it occupied in the hindbrain, becoming more flattened dorso-ventrally, however, and soon moving away from the raphe to a somewhat more lateral position, where it may be traced up into the thalamus.

In the dorsal part of the tegmentum, on the other hand, the medial longitudinal bundle likewise continues forward in the same position where it was observed farther back. It also becomes more flattened dorso-ventrally, and it breaks up into a number of distinct, compact, little bundles. At the level of the trochlear nucleus, it forms a dorsal concavity containing the nucleus, and some of its fascicles run right through the latter (Pl. XIII.). Then it swings round dorso-medially so that at the level of the more anterior part of the oculomotor nucleus the tracts of the two sides enclose between them a V-shaped area of the central gray, in which the nerve nuclei lie. In front of these nuclei, the ventral edges of the two tracts separate a little before they continue into the hypothalamus. Here the tract disappears in relation with a small group of cells, the *interstitial nucleus* of Cajal, situated at the anterior extremity of the red nucleus (vide infra) and just lateral to the tract itself (Pl. XV.). This nucleus gives rise to the *interstitio-spinal tract* (*Tract of Boyce*), which in the rat is a bundle of coarse fibres running back in first the dorsal and then the medial part of the medial longitudinal fasciculus. It gives off fibres to the eye-muscle nuclei and passes on into the spinal cord, taking up a sulco-marginal position there (Papez). In the lateral part of the medial longitudinal bundle, for a considerable distance through the midbrain, run secondary fibres from the nucleus of Deiters to the oculomotor and trochlear nuclei (ascending tract of Deiters).

Extending obliquely between the medial longitudinal bundle and the lateral lemniscus, lies the cross section of the superior cerebellar peduncle, which is thick and rounded dorso-medially (caput brachii conjunctivi) and tapers out almost to a point ventro-laterally (cauda brachii conjunctivi) (Pl. XII.). Passing upward, the cauda becomes less definite and the whole tract becomes a little more medial in position by the time it reaches the level of the trochlear nucleus, about the front of which it turns medially and decussates immediately ventral to the medial longitudinal bundle (Pls. XIII., XXVI.). In the upper part of its course before decussation, it is less sharply marked off from the surrounding reticular formation than farther back. In man, the superior peduncle is proportionally larger than in the rodent and the dense decussation has a considerably greater dorso-ventral extent.

After decussating, the tract runs straight forward a short distance to end largely in the *red nucleus* (*nucleus ruber*) (Pls. XIV., XXVI.). Some of the fibres pass on into the thalamus, while a few turn backward in the reticular formation (*brachium conjunctivum descendens*).

The red nucleus is a large group of cells which is very conspicuous in sections prepared with cytoplasmic stains. In the human brain, it is conspicuous also in Weigert preparations, where it is marked off sharply from the surrounding reticular formation by a capsule made up largely of the fibres of the brachium conjunctivum. In the rat, however, there is no such definite capsule and a great many white fibres run between the cells, so that the nucleus is less sharply delimited in Weigert sections. A magno-cellular division and dorso-lateral and ventro-lateral divisions composed of smaller cells may be distinguished in this nucleus, the magnocellular portion being relatively larger in the rat than in man. Besides the cerebellar peduncles, fibres from the cerebral hemispheres also end in the red nucleus.

From the magnocellular division of the red nucleus, arise

descending fibres which convey to the motor columns of the spinal cord the impulses received from the cerebellum— impulses which are believed to be important factors in muscular coördination and in the maintenance of muscle tone. These fibres pass ventro-medially to cross the raphe as the *ventral tegmental decussation (fountain decussation of Forel)*, after which they turn posteriorly, forming the *rubro-spinal tract (fasciculus rubro-spinalis)* in a position ventro-medial to the red nucleus. Farther back than this nucleus, the tract passes gradually in a lateral direction to a location just ventral to the cauda of the brachium conjunctivum. Papez describes its descending course in the rat as "medial to the lateral lemniscus, ventral to the trigeminus, facial nucleus, etc.".

From the small-celled portions of the red nucleus, arise crossed and uncrossed fibres to other parts of the tegmentum and to the thalamus. From the latter, the impulses are transmitted to the corpus striatum and cerebral cortex. As a result of these relations, the small-celled region is found to correspond in size with the degree of development of the cerebellar hemispheres and of the cerebral cortex (especially the frontal cortex), both of which are small in the rat.

Dorsal to the ventral tegmental decussation and the decussation of the superior cerebellar peduncles, is another group of fibres crossing the raphe. These fibres arise in the tectum, whence they curve round the central gray matter to its ventral surface (*fountain-like radiation of Meynert*) and form the *dorsal tegmental decussation (fountain decussation of Meynert)*. They then turn directly posteriorly, just lateral and ventral to the medial longitudinal bundle, as the tecto-spinal tract, which has already been observed in the hind-brain. Some of the fibres are said by certain authors not to decussate but to pass posteriorly on the same side along with the lateral lemniscus. After giving off fibres to the oculomotor and trochlear nuclei, the tecto-spinal tract suddenly becomes

more scattered near the posterior end of the decussation of the brachia conjunctiva, some of its fibres as they continue back being mingled with the medial longitudinal bundle and with the medial lemniscus (Papez).

The central gray matter surrounding the aqueduct of Sylvius contains several more or less distinct cell-masses. Among the most important of these are the nuclei of the fourth and third nerves, which lie in the ventral part of the central gray, directly dorsal to the medial longitudinal bundle. The *trochlear nucleus* is a small group of large cells in the posterior part of the midbrain (Pl. XIII.). In the rat, it lies actually between the fascicles of the medial longitudinal bundle, suggesting the intimacy of its relation to this tract, from which it receives most of its afferent fibres. The axons arising from this nucleus may be traced postero-laterally and dorsally, running backwards at the boundary between the central gray and the surrounding tissue (Pl. XII.). This course takes the root to the antero-lateral region of the anterior medullary velum, in which the fibres decussate to form the peripheral nerve roots (Pl. XXVI.).

The oculomotor nucleus lies directly in front of the trochlear, being practically continuous with it but entirely dorsal to the medial longitudinal bundle (Pl. XIV.). It extends up to near the anterior end of the midbrain. The root-fibres pass ventrally in small fascicles which emerge along the medial margin of the cerebral peduncles (Pls. XIV., XXVI.), a few of them first decussating between and dorsal to the nuclei and joining the root of the other side. In man, the oculomotor nuclei consist of a median centre (nucleus of Perlia) and paired lateral nuclei. The former, however, is not present in rodents. Immediately dorsal and anterior to the oculomotor nuclei proper, is a mass of small cells the axons of which also emerge in the third nerve. This is the *nucleus of Edinger-Westphal*, which is the origin of the general visceral fibres in the oculomotor nerve. It is continuous

across the median plane in the rodents, but in man is distinctly paired.

The close association of the oculomotor and trochlear nuclei with the medial longitudinal bundle is a significant example of neurobiotaxis (p. 49), this tract containing the majority of the fibres which carry stimuli to their cells.

Various correlation nuclei also occur in the tegmentum, among which, two important centres are the *dorsal and ventral tegmental nuclei* (*nucleus tegmenti dorsalis* or *nucleus ventralis grisea centralis*, and *nucleus tegmenti ventralis* or *nucleus of v. Gudden*). These occur at the extreme posterior end of the midbrain and are better developed in the rodents than in man (Pl. XII.). The dorsal nucleus lies immediately dorsal to the medial longitudinal bundle, a little behind the trochlear nucleus. Between the levels of Pls. XI and XII it appears as a large rounded mass rather clearly outlined by a diffuse capsule of fine fibres. It receives fibres from the interpeduncular nucleus through the tegmental tract of that centre and from the mamillary body through the *mamillo-tegmental tract* (*tractus mamillo-tegmentalis, tract of v. Gudden*). Its axons descend in a system of scattered longitudinal fibres close to the ventricular surface (*dorsal longitudinal bundle of Schütz, periependymal longitudinal tract*), which extends back from the thalamic region but is most distinct at and behind the level of this nucleus. The ventral nucleus is a conspicuous mass ventral to the medial longitudinal bundle, in which also many mamillo-tegmental fibres end. These nuclei are apparently relay-stations on a reflex pathway from the hypothalamus to the motor nuclei of the hindbrain. The mamillo-tegmental tract is difficult to distinguish in the lower part of its course in transverse sections prepared by Weigert's method. It is a group of fine fibres which curve backward in the vertical plane after leaving the mamillary body, and run dorso-posteriorly through the tegmentum on each side of the raphe, to end in the nuclei just described.

Other correlation centres are the dorsal nucleus of the raphe, which lies in the median plane just dorsal to the trochlear nuclei, some groups of cells in the raphe posterior to the decussation of the brachia conjunctiva, and a number of nuclei in various parts of the reticular formation which are not usually distinct in Weigert sections. Among the last of these, there must be mentioned particularly the *nucleus of Darkschewitsch* (Pl. XV.). This mass of small cells is situated at about the level of the anterior end of the medial longitudinal bundle, to which it may contribute some fibres. It lies just dorsal to the interstititial nucleus of Cajal and is probably related particularly to the fibres of the posterior commissure (p. 71).

Situated in a median position at the ventral surface of the tegmentum, lies the *interpeduncular nucleus (ganglion interpedunculare)*, a mass of gray matter occupying the posterior perforated space of human anatomy, which lies at the bottom of the interpeduncular fossa (Pls. XIII., XIV., XXVI.). This centre receives a large fibre-bundle, the *fasciculus retroflexus* of Meynert (Pls. XIV.-XVIII., XXVI.), from each of the habenular nuclei of the diencephalon, and gives off fibres, as already mentioned, which run to the dorsal tegmental nucleus as the *tegmental tract of the interpeduncular nucleus* (Pl. XIII.). This is a group of very fine fibres which may be observed to leave the dorsal surface of the interpeduncular nucleus and to run dorso-posteriorly on each side of the raphe. These structures, being concerned with the correlation of olfactory with other, chiefly somatic, impulses, are largest in animals having a highly developed sense of smell. They are considerably larger in the rat than in man, whose olfactory sense is rather poorly developed.

A bundle which is rather distinct in the ventral part of its course, but of which the origin is still uncertain, becomes visible just behind the mamillary body. This is the *transverse peduncular tract* (Pl. XV.). It probably contains some optic

fibres, and Edinger believed it to be composed largely of
fibres belonging to the ciliary portion of the oculomotor.   It
runs along the medial edge of the pes pedunculi and then
turns dorsally a short distance to end in a centre close to the
substantia nigra and posteroventral to the red nucleus
(*nucleus tractus pedunculi transversus, ganglion ectomamillare*
of Wallenberg).   Kosaka and Hiraiwa found that removal
of the eye of the rat produced degeneration of this tract,
chiefly contra- but partly homo-laterally.   Some of the fibres
enter the subthalamic nucleus.   The secondary fibres from
the nucleus of the transverse peduncular tract are probably
short, running forward into the subthalamic nucleus for
reflexes of the pupil, eyelid, etc.

Just in front of the level of the anterior border of the pons,
there appears a mass of gray matter separating the teg-
mentum from the ventrally situated basis pedunculi.   This
mass is the *substantia nigra*, which has the form of a broad,
thick band extending forward into the hypothalamus, and
becoming thicker and more rounded in cross section as it
does so (Pls. XIV.-XVI.).   It receives fibres from the cerebral
hemispheres and gives rise to others which run through the
tegmentum, but its precise connections and function are
not clearly understood.   It has received its name on account
of its dark colour in the human brain, where it stands out
conspicuously when examined in gross material.   This colour
is due to the presence in many of the cell-bodies of large
numbers of brown pigment granules.   There is less pigmenta-
tion in lower mammals than in higher ones, however, (Kap-
pers) and in the rat it is practically entirely absent.

The basis pedunculi is composed of a broad band of closely-
grouped, longitudinal fibres running along each side of the
ventral surface of the midbrain, and appearing roughly
crescentic in cross section (Pls. II., XIV.-XIX.).   The fibres
originate in the cerebral cortex and pass through the internal
capsules to form these bands, which converge towards the

upper edge of the pons and penetrate into it. These large bundles gradually decrease in size as they descend, giving off fibres to various parts of the brain, and analysis shows that they are composed of several distinct tracts. In man the medial fifth of the bundle is composed of fibres running from the frontal cortex to the pontine nuclei—the *fronto-pontine tract*—but this portion may be presumed to be very small in the rat if it is present at all, as the frontal cortex is developed to a very slight extent. The lateral fifth in man is made up of fibres from the temporal and occipital lobes to the same nuclei—the *temporo-pontine tract*. These two together form the *cortico-pontine tract*. Between these lies the large *cortico-spinal tract*, with which are mingled many *cortico-bulbar fibres*. Many of the latter, however, are grouped in the mid-brain into two distinct bundles, which pass to the nuclei of the cranial nerves.

As might be expected, the basis pedunculi, consisting of fibres of neocortical origin, varies in size in different animals according to the development of the neocortex. It is largest in man, where the neocortex is most highly developed, and is considerably smaller in the rat.

The tectum is the dorsal portion or roof of the midbrain. In the lower vertebrates, it is moulded into two rounded optic lobes, where terminate most of the fibres of the optic nerve, while the posterior part of its ventro-lateral portion contains a more or less massive auditory correlation centre. In the mammals, the latter centre has acquired a more dorsal situation and appears as a second, usually smaller eminence behind the reduced optic lobe. Hence the optic lobes have come to be known in mammals as the *anterior (superior) corpora quadrigemina* or *anterior (superior) colliculi*, while the new eminences are the *posterior (inferior) corpora quadrigemina* or *posterior (inferior) colliculi*. In the rat and other lower mammals, the latter are considerably smaller than the former, while in man they are more nearly alike in size. This

difference in proportion is due chiefly to a decrease in the
functional importance and consequently in the relative size
of the anterior colliculi in man, a much larger percentage of
the optic fibres ending in the diencephalon, whence their
impulses are sent to the cerebral cortex.

As seen in sections, the posterior colliculi appear simpler
in structure than the anterior ones. Each contains a large,
somewhat rounded mass of gray matter, the *nucleus of the
posterior colliculus*, which is the end station of the greater
part of the lateral lemniscus (Pls. XII., XIII.). Most of the
fibres of this tract may be seen to plunge directly into the
nucleus. Some of them, however, pass round it, forming a
capsule, before entering its substance. A certain proportion
of these may decussate, to end in the nucleus of the other
side, but Papez finds no evidence of this in his studies of
degeneration in the brain of the rat.

Separated from the nucleus of the posterior colliculus by
the deep portion of its capsule together with a mass of fibres
arising in the tectum (*stratum profundum*), lies a thick layer
of central gray matter. Dorsal to this, the space between
the two nuclei is filled by *internuclear cortex* or *laminated
gray matter of the tectum*, which is penetrated by a great many
transverse white fibres.

The tectum being composed of important reflex corre-
lation centres, it receives many different kinds of fibres,
coming from the spinal cord, the medulla oblongata, and the
forebrain. These, however, are not easily traced in ordinary
sections. On the other hand, efferent fibres are said to leave
the tectum for all of these regions of the central nervous
system. Axons arising both in the nuclei of the posterior
colliculi and in the laminated gray matter form a layer
between these and the central gray (stratum profundum) in
which they are said to run ventrally to the tegmentum to
join the tecto-bulbar and tecto-spinal tracts. Papez, however,
can find in Marchi preparations of rat brains no demonstrable

descending tract from the posterior colliculi, and concludes that these cannot be regarded as reflex centres. Many of these fibres decussate between the two corpora quadrigemina as the *commissure of the posterior colliculi* and Papez finds these to end entirely in the opposite colliculus. Along with the commissure of Probst and the incomplete decussation of the trapezoid body, they provide for bilateral representation of auditory stimuli in the posterior colliculi and in the medial geniculate bodies. Many fibres arising in each posterior colliculus, moreover, enter its brachium (vide infra) to ascend to the thalamus.

Not all the fibres of the lateral lemniscus end in the posterior colliculi. Some divide before terminating there and send a branch into the anterior colliculus, and it may be that a few such fibres end in the latter region without previously dividing. A considerable number of the fibres terminating in the colliculi are, moreover, collaterals from axons which continue their course farther up the brain along with some which have no connection in the midbrain. These form a distinct tract on the lateral aspect of the tectum, which is the direct continuation of the lateral lemniscus, but which is now known as the *brachium of the posterior colliculus* or *posterior (inferior) quadrigeminal brachium* (Pls. XII.-XV.). The fibres which end in the tectum form the chief reflex auditory pathway, according to the usual view, while the brachium is the cortical pathway, up which pass auditory impulses destined to enter consciousness. The fibres of the latter group end in the medial geniculate body, whence new axons pass to the auditory cortex. The brachium contains also fibres arising in the posterior colliculi, and some of cortical origin which terminate in these centres.

The nucleus and fibres of the mesencephalic root of the trigeminal nerve, which lie in the lateral part of the tectum at the outer border of the central gray matter, have already been described.

The anterior colliculi show a distinct lamination—a character which is evidently very ancient and fundamental, since it is found in the optic lobe of all vertebrates except the cyclostomes and tailed amphibians. In the mammals, the lamination is less complex than in lower forms, the reduction being chiefly in the outer layers; and in the lower mammals, such as the rat, these layers are more largely developed than in man, the purely reflex visual responses being of more importance in the rat than in man. The cortex of the anterior colliculi is considered to be made up of four layers, though secondary divisions may be distinguished in these (Pls. XIV.-XVI.). The surface is covered by a very thin layer of fibres, the *stratum zonale*. Below this come in order the much thicker *stratum griseum*, which contains very few myelinated fibres, and the thick *stratum opticum* and *stratum lemnisci*, in which end respectively fibres belonging to the systems indicated by their names, along with many others. The two latter laminae both contain large numbers of myelinated fibres. The *stratum profundum* separates the stratum lemnisci, from which it is not sharply differentiated, from the central gray matter and is made up chiefly of efferent fibres from the superposed laminae, particularly from the stratum griseum. The efferent fibres in the stratum profundum mostly enter the dorsal tegmental decussation, after crossing in which they form the tecto-spinal and -bulbar tract, though some of these fibres are stated to descend without crossing. Stratum profundum fibres crossing the middle line form the *commissure of the anterior colliculi*.

Near the anterior end of the tectum, the fibres of the optic tract (here called the brachium of the anterior corpora quadrigemina) may be observed entering the stratum opticum, and deeper than these are many fascicles which Cajal believes to come from the cerebral cortex (cortico-tectal tract). These form a distinct layer in the deeper portion of the stratum opticum.

Not only are the anterior colliculi much larger in the rat than in man, but the structural differentiation within them, as just described, is much more marked.

At the anterior boundary of the tectum, where it continues into the thalamus, lies the large *posterior commissure* (*commissura posterior*), which appears as an anterior extension of the stratum profundum of the anterior corpora quadrigemina (Pls. XVI., XVII., XXVI.). This commissure is apparently a rather fundamental structure as it is very constant throughout the whole vertebrate series and develops early in ontogeny. Nevertheless its relations and functional significance are not yet clearly understood. At each side of the commissure, its fibres spread out in a large mass of cells which has been called the *nucleus of the posterior commissure*, and which is continuous with an elongated cell mass in the deep layers of the optic tract and with the deeper parts of the anterior colliculus. The nucleus of the posterior commissure receives optic tract fibres and gives rise to a large part of the commissure itself in the rat. Papez is inclined to believe that the commissural fibres rising in this centre terminate exclusively in the region of the interstitial nucleus or the nucleus of Darkschewitsch on the other side, thus leading from the optic tract to the heterolateral interstitio-spinal tract. Another important constituent of the commissure is probably made up of ascending vestibular fibres from the lateral part of the medial longitudinal bundle, and there may also be contributions from the posterior nucleus of the thalamus (p. 82) and from the nucleus of Darkschewitsch.

The Diencephalon.

AT the anterior extremity of the midbrain, the appearance of sections changes considerably as one passes forward into the next region, the 'tweenbrain, 'twixtbrain, or diencephalon. At this point, the aqueduct of Sylvius opens out into the third ventricle, which has the form of a high, narrow slit with a rather thin floor, a membranous roof, and an exceedingly massive wall at each side.

The diencephalon has three main subdivisions, the *epithalamus*, a small dorsal region; the *hypothalamus*, a small ventral region; and between these the extensive *thalamus*, including the geniculate bodies, which are sometimes distinguished as the *metathalamus*.

The epithalamus comprises the thin, membranous roof of the third ventricle, the pineal body, and the habenulae. The first of these is thrown into folds and richly supplied with blood vessels forming the *chorioid plexus of the third ventricle*. The *pineal body* or *epiphysis* is a small, unpaired glandular body which projects back between the anterior corpora quadrigemina, with the posterior portions of the cerebral hemispheres largely covering it from the sides (Pl. I.). It is attached by a short stalk to the posterior portion of the roof of the third ventricle, where a commissure connects the habenulae.

The *habenula* is a paired centre which has the form of a fusiform ridge along the dorsal edge of the wall of the third ventricle where the membranous roof is attached (Pls. XVIII.-XX., XXVI.). In section, it is seen to consist of a column of gray matter covered dorsally and ventrally by layers of

white fibres and composed of two distinct nuclei. These
nuclei are a larger, lateral mass of rather scattered cells with
many myelinated fibres and a smaller, medial group of many,
closely-packed, smaller cells with few white fibres. Anteriorly,
the medial nucleus divides into dorsal and ventral portions,
in the rat, while posteriorly it is continuous with that of the
other side through the poorly-developed bed nucleus of the
habenular commissure. The dorsal layer of white matter is
a definite band composed of compact bundles of longitudinal
fibres, the *stria medullaris thalami*, of which the medial edge
projects slightly into the membranous roof as the *taenia
thalami*. The latter forms a small but sharp ridge marking
the dorsal extremity of the wall of the third ventricle. It is
composed of olfactory fibres of various kinds (see below), all
of which probably end in the nuclei habenulae, so that the
stria medullaris diminishes in size as it passes posteriorly.
Many of its fibres, nevertheless, are still to be seen just
behind the posterior end of the nucleus. These cross the
middle line directly dorsal to the posterior commissure to
terminate in the habenular nucleus of the other side, thereby
constituting the *habenular commissure* (*commissura habenu-
larum, superior commissure*) (Pls. XVII., XXVI., drawn but
not named in Pl. III.), which is small in the rat. Traced
anteriorly, the stria medullaris is seen to turn ventrally at
the anterior end of the thalamus and to spread out in the
ventro-medial part of the hemisphere, where it meets the
longitudinal fibres of the diffuse medial forebrain bundle.

A summary of the composition of the stria medullaris of the albino
rat has been given by Herrick,[1] who lists eight component tracts, as
follows:

(1) Tractus olfacto-habenularis medialis—composed of fibres from the
praeoptic nucleus and surrounding gray matter. There are anterior and
posterior parts of this tract running respectively in front of and behind the

[1] "The conclusions as I published them should be accepted with some
reserve, though I believe them to be substantially correct". (Herrick—
personal communication.)

column of the fornix, and there may be also a small lateral portion passing up lateral to the fibres of the internal capsule.

(2) Tractus olfactohabenularis anterior—the largest component in the rat. The fibres arise in the tuberculum olfactorium and pass backward with those of the medial forebrain bundle (p. 97) to the level of the optic chiasma, where they turn dorsally.

(3) Tractus septohabenularis—made up of fibres from the entire septal region in the broad application of that term (p. 93), especially from the portion near the anterior commissure.

(4) Tractus corticohabenularis medialis—composed of fibres arising in the hippocampus and passing through the fimbria and column of the fornix. They leave the latter for the stria medullaris when these structures pass close to each other near the anterior commissure. They are drawn on the lateral surface of the column of the fornix in Plate XXI, but are not named.

(5) Tractus corticohabenularis lateralis—fibres coming from the pyriform lobe, nucleus of the lateral olfactory tract, and tuberculum olfactorium running dorsomedially and converging with component (2) to enter the stria medullaris (Pl. XX., sma).

(6) Tractus thalamohabenularis—consisting of fibres from the anterior thalamic nucleus running through the stratum zonale thalami (the thin superficial fibre layer) into the stria medullaris.

(7) Tractus striohabenularis—fibres between the stria medullaris and the medial part of the globus pallidus (p. 106)—connections unknown.

(8) Imperfectly known connections between the habenula on the one hand and the thalamus and the midbrain on the other.

Apparently not included in this classification is (9) the stria medullaris bundle of the stria terminalis which arises in the pyriform lobe, the nucleus of the lateral olfactory tract, and the tuberculum olfactorium, according to Johnston, runs through the stria terminalis, and joins the stria medullaris near the anterior commissure.

Gurdjian has recently confirmed for the rat the description of components (1)—(5) and (9). He describes hypothalamic fibres in component (1) and intimate synaptic relations between components (3), (4) and (9) and the bed nuclei of the anterior commissure and the stria terminalis.

In the stria medullaris, components (3) and (4) lie dorsally, (4) medial to (3), and components (1), (2) and (5) ventrally and medially, (1) being most ventral.

Many of these connections are indicated in Fig. 4.

The efferent fibres of the habenula take up a position ventral to the nucleus, where they descend to near its pos-

terior extremity, then, turning sharply ventrad, they run
straight to the interpeduncular nucleus as the fasciculus
retroflexus (Pls. XIV.-XVIII.). Thus the habenular nuclei
are a relay station on the descending olfactory pathway and
probably serve for the correlation of the olfactory impulses
with somatic sensory ones received from neighbouring parts
of the thalamus (Herrick). This whole system, as already
pointed out, is considerably larger in macrosmatic animals,
such as the rat, than in microsmatic forms, such as man.

The hypothalamus forms the floor of the third ventricle,
and comprises the *pars optica hypothalami*, the *tuber cinereum*
and the *infundibulum*, and the *mamillary bodies*. The pars
optica hypothalami is part of the telencephalon and will
therefore be considered later.

The mamillary bodies are a pair of rounded eminences
at the posterior extremity of the ventral surface of the dience-
phalon in the human subject. In the rat, however, as in
many other lower mammals, the two bodies are fused into
a single median mass (Pls. II., XV., XXVI.). This fusion
is not only external but also internal, the bodies being separ-
ated in man by a ventral extension of the third ventricle
which does not occur in rodents.

Superficially, the bodies are covered by a very thin capsule
of white fibres. Each mamillary body consists of two main
nuclei, a larger medial one and a smaller lateral one, and
between these penetrates a great mass of descending olfactory
fibres of the fourth order—the *column of the fornix* (*columna
fornicis*) (Pls. XV.-XXII.). Many of these fibres (or at least
many collaterals from them) end in the mamillary nuclei.
Others, however, pass dorso-medially, becoming more scat-
tered as they do so, and form a diffuse decussation (*the supra-
mamillary decussation*) (Pl. XV.), after which they descend
through the tegmentum.

Another tract belonging to the mamillary body which is
well developed in the rat, and which is probably afferent, is

the *peduncle of the mamillary body* (*pedunculus mamillaris, tractus mamillo-peduncularis*). This fasciculus ascends from the hindbrain along the ventral surface, just medial to the pes pedunculi (Pls. XIV., XV., XXVI.). It enters the mamillary body dorso-lateral to the column of the fornix and bifurcates there, sending many transverse fibres dorsal to the fornix into the medial nucleus, while the rest of the tract passes ventrally into the lateral nucleus.[1] It can be traced back down the brain to about the level of the most posterior roots of the oculomotor nerve, where it joins the medial lemniscus, with which at least some of its fibres have evidently ascended. The mamillary body also receives afferent fibres from the tuberculum olfactorium, etc., through the olfacto-hypothalamic tract.

The efferent fibres of the mamillary body leave the antero-dorsal part of the medial nucleus as a group of compact bundles which form a conspicuous tract running anteriorly and dorsally to end in the anterior nucleus of the thalamus (p. 82). This tract is the *mamillo-thalamic tract* or *bundle of Vicq d'Azyr* (*fasciculus mamillo-thalamicus*) (Pls. XV.-XX., XXVI.). Shortly before reaching its terminal nucleus, it breaks up in the rat into many small scattered bundles, so that it becomes much less evident than it is in the preceding part of its course. The early course of these fibres is not straight, however, as is strikingly evident in sagittal sections. They curve rapidly upwards until they are running nearly vertically, when many of them bifurcate, the one branch turning sharply forward in the mamillo-thalamic tract, while the other continues its sweeping curve and takes a posterior direction across the medial surface of the fasciculus retroflexus and back to the dorsal nucleus of the tegmentum. There, it has already been described as the mamillo-tegmental

[1] A few fibres from this tract continue forward into the tuber cinereum in the rat. A lesion in the peduncle in this animal produces no descending degeneration (Papez).

tract (Pls. XII.-XVI., XXVI.). This fasciculus is considerably smaller and less conspicuous than the mamillo-thalamic tract. It probably conveys effector impulses which are perhaps concerned with the act of sniffing.

Anterior to the mamillary bodies, is more gray matter, which forms the tuber cinereum, and from which there projects ventrally the hollow stalk of the hypophysis, the infundibulum (Pls. XV.-XVIII.). The tuber cinereum, like the mamillary body, receives olfactory and other fibres, and these two regions together constitute an important olfactory correlation area, which is probably chiefly olfacto-visceral in function. The mamillo-tegmental tract leads the resultant nerve impulses down towards the motor centres, while the mamillo-thalamic tract conducts similar impulses to the anterior thalamic nucleus, where they are further correlated with others of somatic origin.

Thus we have in the epithalamus olfacto-somatic correlation, in the hypothalamus olfacto-visceral correlation, and in the anterior thalamic nucleus olfacto-viscero-somatic correlation.

The thalamus is made up of dorsal and ventral parts, of which the former is very much larger in mammals than is the latter.

The ventral part is the *subthalamus*, which has sometimes been confused with and sometimes included in the hypothalamus. Its phylogenetic history, however, seems to show that it should be regarded as a ventral part of the thalamus, of which it is the motor coördination centre.

The subthalamus is the direct forward continuation of the substantia nigra of the midbrain and the reticular formation just dorsal to it. It is not so large in the lower mammals as in man and the primates, though this fact does not strike the observer on account of the still greater enlargement in the latter forms of the dorsal part of the thalamus. The ventral region is by no means simple, though not very large,

and its structure and connections have not yet been thoroughly elucidated. The outstanding structures in it which are usually described are as follows.

The *subthalamic nucleus* (*corpus subthalamicum, body* or *nucleus of Luys*) is particularly large in primates. It appears in the human brain as a rather conspicuous, lens-shaped nucleus lying immediately dorsal to the pes pedunculi. In the rat, however, it is not clearly marked off from surrounding structures in Weigert preparations. It has the general form of a flattened mass of numerous rather large cells, penetrated by many medullated fibres and occupying about the same position as in man (Pls. XVII., XVIII.). The centre is marked in the figures according to the description of Cajal and a comparison of Weigert and Nissl sections of the rat brain with Weigert sections of human material. This mass appears to be the *nucleus proprius pedunculi cerebri* as identified by Winkler and Potter,[1] who indicate a more diffuse group of cells dorso-lateral to this as corpus subthalamicum.

Dorsal to this region is the *zona incerta* (Pls. XVII.-XIX.), which in man lies between two distinct layers of white fibres belonging, like the capsule of the subthalamic nucleus, to the *ansa lenticularis*. In the rat, the fibres form a diffuse net among the small cells of the region, which thus lacks, like the subthalamic nucleus, the clearly marked boundaries in Weigert sections which are seen in the human brain. The ansa lenticularis probably contains both ascending and descending fibres between the corpus striatum of the cerebral hemisphere and the corpus subthalamicum and neighbouring gray matter.[2] Anteriorly this area continues beyond the

[1] An Anatomical Guide to Experimental Researches on the Rabbit's Brain. Amsterdam, 1911.

[2] Morgan (Anat. Rec., vol. 29, p. 369) has recently called attention to a tract in man running from the ansa lenticularis dorsally, medial to the red nucleus, close to the mamillo-tegmental tract, and taking up a position immediately lateral to the medial longitudinal bundle. While

frontal extremity of the subthalamic nucleus as a similar looking region known as the *regio innominata*, in which run a large number of thalamic fibres to and from the cerebral hemispheres.

Perhaps to be included with the subthalamus (Herrick '18), is the *nucleus reticularis thalami* (*formatio reticulata, lattice nucleus, radiate nucleus*), which occurs between the zona incerta and the overlying white fibres (ventral medullary lamina) in the more anterior part of the extent of the former. It is continuous with a more lateral portion in the lateral part of the thalamus and anteriorly extends between the nucleus anterior and the fibres of the internal capsule (Pls. XIX., XX.). Its names are derived from the many large bundles of cortico-thalamic and thalamo-cortical fibres which run through it.

The dorsal portion of the thalamus is very large as compared with the parts of the diencephalon hitherto considered, this disproportion being even much greater in man than in the lower mammals. The great increase in size is correlated with the development of the cerebral cortex, the increase being chiefly in those parts which serve as relay stations on the sensory paths to the hemispheres—and every such path is interrupted by a synapse in the thalamus.

One of the first parts of the thalamus to appear as one passes forward in serial sections is the *medial* or *internal geniculate body* (*corpus geniculatum mediale*), which forms a marked eminence on the lateral surface of the brain near the frontal end of the anterior colliculi (Pls. III., XV.-XVII.). The nucleus is surrounded and penetrated by many white fibres, largely derived from the brachium of the inferior colliculus, which ends in this centre. Thus the body receives auditory impulses, and these it transmits along its axons to the auditory area of the cerebral cortex. Not all its axons

these fibres are not very distinct in the writer's preparations of the rat brain, they appear to be present between the levels of Plates XIV and XV.

run to the cortex, however, some passing to the region of the optic chiasma, in the posterior part of which they decussate as the *commissure of v. Gudden* or *postoptic commissure* (*commissura supraoptica ventralis*), and then running back to the medial geniculate body or posterior colliculus of the opposite side. The fibres of this commissure are rather fine and lie in the ventro-medial edge of the optic tract.

Covering the antero-dorsal aspect of the medial geniculate body is the large, curved *lateral* or *external geniculate body* (*corpus geniculatum laterale*), which is the terminal nucleus for a large number of the fibres of the optic tract (Pls. III., XVII., XVIII.). The latter forms a covering of white matter over the outer surface of the nuclear mass, into which a large proportion of its fibres are seen to plunge, while the remainder pass on to enter the anterior quadrigeminal body. The percentage of the optic fibres ending in the geniculate body is, as we have seen, smaller in the rat than in man, corresponding with the relative functional importance of the cortical connections in the two cases. The difference is not so great as it might have been, however, on account of the fact that a considerable part of the rodent geniculate body does not serve, apparently, as a relay station to the cortex. In the rat and other lower mammals, the lateral geniculate body consists of distinct dorsal and ventral nuclei (Pl. XVIII.), of which only the dorsal one sends its axons to the cerebral cortex. The ventral nucleus perhaps transmits its impulses to the tectum of the midbrain. As one examines forms higher in the mammalian series, the dorsal nucleus is found to increase in importance and the ventral one to decrease, until in man the latter cannot be recognized. The dorsal nucleus in man, on the other hand, is greatly developed and shows a lamellated structure with crossed and uncrossed fibres ending in alternate layers. The fibres arising in the dorsal nucleus form the *radiatio optica* or *optic radiation*, which joins the

internal capsule. The radiation contains descending as well as ascending fibres.

In man, some optic fibres end in the pulvinar, where they meet fibres from the cerebellum, and whence impulses are transmitted to the cerebral cortex. This centre, however, which forms a large mass projecting back over the antero-lateral aspect of the anterior quadrigeminal bodies in the human brain, is not developed in the lower mammals. It is a part of the lateral nucleus of the thalamus (vide infra p. 85).

The optic chiasma itself belongs to the telencephalon. The optic tracts and the nervous portions of the eye originate developmentally from the wall of the diencephalon, however, and the fibres end, as we have seen, either in the diencephalon or in the midbrain, so that the chiasma also may reasonably be considered at this point. It lies immediately in front of the di-telencephalic boundary on the ventral surface of the brain, and is composed essentially of the decussating fibres of the optic nerves. These arise in the retina and most of them cross over and pass to their terminal centres on the other side. Some of the fibres, however, coming from the lateral (in man) or posterior (in animals with the eyes in the sides of the head) side of the retina, do not decussate, but run through the homolateral optic tract to their termination. The exact proportion of the fibres which cross over varies in different animals according to the degree of overlapping of the fields of vision of the two eyes. In man, where there is a maximum of overlapping, about one quarter of the optic fibres are uncrossed, but in the rat the proportion is much smaller.[1] The uncrossed fibres in the rat are scattered among the crossed ones in the optic tract except near the chiasma, where they are grouped chiefly in the dorsal part.

The optic fibres are accompanied in the chiasma by the commissure of v. Gudden, which was discussed above, and

[1]But larger than in the rabbit.

by the *commissure of Meynert* (*commissura supraoptica dorsalis*). The latter is better developed in the rat than in the human species and forms a conspicuous decussation postero-dorsal to the optic fibres. It is composed of fine fibres, which may be observed running along the medial aspect of the optic tract (Pl. XVIII.). These fibres are probably telencephalic, but their exact relations are still uncertain.

A small, aberrant bundle of optic fibres is separated from the rest by the commissures of v. Gudden and Meynert, crossing in the most posterior part of the chiasma. They gradually penetrate these commissures, however, and pass through them to join the main optic tract, a few ending in the subthalamic nucleus.

There may perhaps be included with the geniculate bodies under the heading metathalamus[1] the *posterior nucleus of the thalamus* (*nucleus posterior thalami, nucleus praebigeminalis*), which is related chiefly to the midbrain and has no ascending cortical connections. It is a rather large group of cells lying medial to the medial geniculate body and the dorsal part of the lateral nucleus at the posterior end of the thalamus (Pls. XVI., XVII.). It receives a group of collaterals from the medial lemniscus.

The remainder of the thalamus falls into three chief divisions, the *anterior, medial*, and *ventro-lateral nuclei*.

The *anterior nucleus* (*nucleus anterior thalami, nucleus dorsalis thalami*) is wedged between the rostral ends of the other two groups and extends farther anteriorly than either of them (Pl. XX.). The bundle of Vicq d'Azyr has already been traced to this nucleus, which receives through it impulses from olfactory centres. Thus it is not surprising to find that the size of the anterior nucleus of the thalamus varies in different animals with the degree of development of the olfactory system, though not related to it alone. Hence

---

[1]According to Kappers. Other writers regard the posterior nucleus as a part of the lateral nucleus.

this nucleus is considerably larger in the rat than in man.
It consists of two distinct cell masses—a smaller, dorsal,
large-celled group and a larger, ventral and lateral, small-
celled group. The anterior thalamic nucleus sends fibres to
the caudate nucleus (p. 105) and probably to the cerebral
cortex and also has connections with the medial thalamic
nucleus. It is probably of special importance in olfactory
exploration.

The anterior thalamic nucleus in the human brain is
separated from the adjacent gray matter by a layer of white
fibres formed by the bifurcation of the dorsal edge of a vertical
plate of such fibres which separates the medial and lateral
nuclei. This layer of white matter is the *internal medullary
lamina* (*lamina medullaris interna thalami*), a very distinct
object in sections of the human thalamus, but very much
less so in that of the rat, through most of which there is a
more or less diffuse scattering of white fibres.

The *medial nucleus* (*nucleus medialis thalami*) (Pls. XVIII-
XX.) comprises several distinct cell groups and probably has
various functions in its different parts. It has both ascending
and descending connections with the corpus striatum and
probably with the cerebral cortex. This group and the
anterior nucleus are the older part of the thalamus phylo-
genetically and contain the intrinsic reflex mechanism of
that region of the brain. The medial nucleus probably
includes among its functions the more primitive and ele-
mentary forms of consciousness.

This mass is separated from the third ventricle in man
by a thin layer of *central gray matter* which contains scattered
cells constituting the nucleus paramedianus. The latter
is probably a visceral—particularly vasomotor—reflex centre.
The enlargement of the thalamus has reduced the ventricle
to a narrow slit and has brought its two walls into contact
over part of their area in a great many cases, forming a con-
tinuous mass of gray matter across the median plane—the

intermediate mass or *soft commissure* (*massa intermedia, commissura mollis, commissura media thalami*) (Pls. XVIII.-XX.).

In the rat and other lower mammals the central gray matter is more largely developed than in man, containing a number of distinct nuclei and having the area of fusion in the intermediate mass extended so as to obliterate a large part of the third ventricle. The chief median mass of cells is given the name of *nucleus reuniens* (*nucleus rhomboidalis*) (Pls. XIX., XX.), though Winkler and Potter confine this term to one of the cell-groups which can be distinguished in it.

Lateral and ventral to the foregoing portions of the thalamus, we observe an extensive region which is a more recent acquisition, from the phylogenetic standpoint. This is the ventro-lateral group of nuclei, which is related in development to the cerebral cortex, its general function being that of an antechamber to the latter, particularly for general somatic sensory impulses. It is divisible into two main parts, ventral and lateral, in each of which a number of nuclei are to be found. The term lateral nucleus is frequently used to include both parts, *i.e.*, the whole ventro-lateral group, but will not be employed in that sense here.

In the human brain, the *ventral nucleus* (*nucleus ventralis thalami*) contains, besides other gray matter, two centres which are very clearly defined in Weigert sections. These are a rather large, round mass, the *nucleus centralis* or *medial centre of Luys* (*centrum medianum, nucleus globosus thalami*),[1] and a curved body just ventral to this, the *nucleus arcuatus* or *nucleus semilunaris* (*corpus patellare*). These, however, do not stand out in the same distinct way in the brains of lower mammals, and the homologies seem not to be certain in many cases. Like the anterior and medial group, the ventral nucleus is not most highly developed in the highest mammals, and it is quite large in the rat (Pls. XVIII.-XX.)

The ventral nucleus receives most of the terminals of the

[1]This is included by Kappers in the medial nucleus.

medial, trigeminal, and spinal lemnisci; the former[1] chiefly medially, the latter laterally, and between them the trigeminal lemniscus, which goes mainly to the nuclei centralis and arcuatus. While the ventral nucleus as a whole gives rise to an extensive cortical radiation, some of its constituent centres seem to have few or no such fibres, and the mass is apparently rather intimately related with the medial nucleus.

The *lateral nucleus*, on the other hand, is overwhelmingly cortical in its connections, and enlarges enormously as the cerebral cortex becomes more extensive. It is thus much smaller in the rat than in man, though the exact functional significance of this difference is not clear. A considerable part of the increased bulk in the higher form is represented in the pulvinar,[2] which is not distinguishable in the rodents.

The lateral and ventral surfaces of the ventro-lateral nucleus are covered by the lattice nucleus (nucleus reticularis thalami) (Pls. XIX., XX.), which is much more extensive in the rat than in man. In the latter it is marked off from the lateral nucleus by white fibres, the *external medullary lamina* (*lamina medullaris externa*), but this lamina is not definite in the rat—chiefly owing to its being more largely developed and scattered through the nucleus.

A conspicuous object in the diencephalon is the crusta of the cerebral peduncle (basis or pes pedunculi), which runs

[1]In the rat, "the principal terminals course along and in the ventral surface of the ventral and lateral nucleus of the thalamus, forming a narrow, crescentic, lemniscal stratum. The degeneration of these terminals is limited almost exclusively to this nucleus". (Papez.)

[2]This is apparently a centre concerned largely with the correlation of optic and cerebellar impulses, though it, no doubt, receives many others. It has a largely developed connection with the cerebral cortex, particularly with the area of the latter which seems to be largely concerned in spacial recognition.

The suggestion has been made that the great enlargement of the lateral nucleus is related to the emancipation of the fore limb, which has reached such importance in the primates, and especially in man.

back on each ventro-lateral aspect of this region to the mid-
brain. It is formed by fibres descending through the internal
capsule lateral to the more anterior parts of the thalamus
and turning back to run to various lower parts of the central
nervous system as has already been described. These are
accompanied by many fibres which end in the thalamus
itself, so that even by the time it reaches the midbrain the
tract is already considerably smaller than when it started.

Telencephalon—Rhinencephalon.

THE telencephalon comprises all those parts of the brain which have not yet been considered—all that lie morphologically anterior to the diencephalon. It consists of a very small median portion which continues the diencephalon forward and encloses the anterior part of the third ventricle, the *telencephalon medium* (*pars optica hypothalami*), and of paired lateral evaginations from this the *cerebral hemispheres*.

Each hemisphere contains a cavity, the *lateral ventricle*, which is connected with the anterior part of the third ventricle by a small *interventricular foramen* (*foramen of Monro*). The roof of the lateral ventricle with the dorsal parts of its walls form the *pallium*, which in mammals has an external layer of gray matter, the *cerebral cortex*, and is greatly expanded so as largely to cover the outer surface of the rest of the hemisphere. What were primitively the floor and more ventral parts of the walls form the *basal ganglia*, which are very largely hidden from view in the gross brain by the expansion of the pallium. Of the structures visible externally, the tuberculum olfactorium belongs to this division, as does also the lower part of the medial wall just in front of the telencephalon medium. This part is known as the *paraterminal body* (*corpus paraterminale seu precommissurale*), or frequently as the *septum*, though the latter term is confined in man to a postero-dorsal extension of this region,[1] as we shall see presently (p. 93).

[1] According to Johnston, the septum pellucidum of higher mammals is not genetically related to the paraterminal body, but is a separate

At the anterior end of each hemisphere is the olfactory
bulb, which is connected by the olfactory tract with masses
of gray matter, both pallial and subpallial (*i.e.*, belonging to
the basal ganglia). All of these, together with the olfactory
centres in the diencephalon, make up the *rhinencephalon* or
olfactory brain.

The olfactory portions of the pallium are the older phylo-
genetically and are given the name *archipallium*,[1] while the
non-olfactory portions are called the *neopallium*. It is the
neopallium which has expanded in the mammals, as mentioned
above, and in the higher mammals it expands a great deal
more, crowding down the other parts until they are almost
completely concealed by it, and becoming very much con-
voluted.

A consideration of the rhinencephalon starts naturally
with the olfactory bulb (fig. 4, Pl. XXV.), which receives the
axons of the olfactory nerve cells lying in the nasal mucous
membrane. Penetrating the anterior and ventral surfaces
of the bulb, these unmyelinated fibres terminate in little,
densely-matted knots called *glomeruli*, each of which contains
the terminal branches of several fibres and also one or more
dendrites from cells of the second order, the *mitral cells*. The
axons of the mitral cells form the olfactory tract, which
conducts the impulses back to the cerebral hemisphere proper
and end there in the secondary olfactory area. Just after
leaving the cell body, however, the axon gives off collaterals
which come into relation with the *granule cells*, small neurons
present in the olfactory bulb in great numbers. The axons
of the latter extend back to the mitral cells and discharge
among their dendrites. This arrangement and the glomeruli
are both to be regarded as mechanisms whereby strong central
impressions may be produced by weak peripheral stimuli.

structure of pallial origin dorsal to the latter, so that the name septum
should not be applied to the paraterminal body. (See Figs. 7 and 8.)

[1] See, however, footnote on p. 97.

All these elements in the olfactory bulb are arranged in definite layers (Pl. XXV.). Superficially, we find, as would be expected, a thin layer of unmyelinated fibres made up of the entering primary olfactory axons (*stratum fibrorum, lamina fibrorum nervi olfactorii*). This passes into a layer in which the glomeruli are seen lying side by side in a single series (*lamina glomerulosa*). A thin band of granule cells (*lamina granulosa externa*) lies just inside this, and a stratum made up of dendrites and unmyelinated fibres (*lamina gelatinosa*) separates the latter from the perikarya of the mitral cells, which are disposed in a single row (*lamina cellularum*). Alternating layers of granule cells and unmyelinated fibres with a few fine myelinated fibres (*lamina granulosa interna*) lie inside the layer of mitral cells, and between the former and the centre of the bulb are two layers of myelinated fibres (*lamina fibrorum tractus olfactorii* and *lamina fibrorum medullae lobi piriformis*). The fibres in the outer of the two last mentioned layers are grouped in little bundles which run together posteriorly to form the olfactory tract. Those in the innermost layer have thinner myelin sheaths, are scattered in a rather diffuse reticulum, and run into the deep white matter of the lateral olfactory gyrus (vide infra). They include the fibres to and from the anterior commissure (p. 97). Among them are many small cells, which are most numerous near the centre, where the ventricle is situated.

Some of the olfactory nerve fibres (the vomeronasal nerve) separate from the rest and run to a small body which is imbedded in the posterior part of the dorsal surface of the olfactory bulb. This is the *accessory olfactory bulb* or *bulbus parolfactorius* (Pl. XXV.). Its structure is similar to that of the olfactory bulb, except that the internal granular layer is nearly absent and the fibres to the olfactory tract lie between the mitral layer and the internal granular layer of the olfactory bulb. These fibres run in the lateral olfactory stria to the amygdaloid complex (p. 92).

If the observer work back through a series of sections of the olfactory bulb, he will see a new mass of gray matter appear just lateral to the layer of fibres of the medulla of the lateral olfactory gyrus. This enlarges backwards and is found to be the *cortex of the lateral olfactory gyrus*, on the lateral aspect of which the olfactory tract is seen, while the olfactory bulb extends some distance back along its ventro-medial aspect.

According to the usual descriptions, the human olfactory tract consists of three parts known respectively as the *medial*, *intermediate*, and *lateral olfactory striae*. The last of these runs into the lateral olfactory gyrus and gyrus hippocampi (which is represented by the pyriform lobe of the rat); the intermediate olfactory stria ends in the intermediate olfactory nucleus, which occupies the anterior perforated area of man and includes a vestige of the large tuberculum olfactorium of lower mammals; while the medial olfactory stria is distributed to the subcallosal gyrus (paraterminal body) and septum pellucidum of man, both of which are represented in the septum of the rat.

The medial olfactory stria is small and diffuse and lies below the surface in the rat, just dorso-medial to the intermediate stria, running back over the anterior part of the tuberculum olfactorium. The intermediate olfactory stria is better developed, but runs along the medial aspect of the lateral olfactory stria in the anterior part of the course of this bundle, so that it does not appear as a distinct structure, the two together forming a single conspicuous *olfactory tract* on the latero-ventral aspect of the brain (Pl. XXIV.).

The olfactory tract (lateral olfactory stria only, in its more posterior part) forms a conspicuous band extending back along the ventral surface of the hemisphere for about half the length of the latter, accompanied by the gradually increasing gray matter of the lateral olfactory gyrus. The depression in the surface of the cerebral cortex occupied by

the olfactory tract is the *endorhinal groove* (*sulcus endo-rhinalis*). At each side of the optic chiasma, the lateral olfactory gyrus expands rather suddenly in a ventro-medial direction, forming the large *pyriform lobe* (*lobus piriformis, lobus sphenoidalis*) with a prominent medial eminence, the *uncus* of human anatomy, and the fibres of the olfactory tract are dispersed in this enlarged lobe. The related gray matter medial to the lateral olfactory gyrus forms the *anterior olfactory lobe* (*intermediate olfactory nucleus*), while the pyriform lobe and the lateral olfactory gyrus make up the *posterior olfactory lobe*. There appears to be no real structural difference between the lateral olfactory gyrus and the pyriform lobe, so that the latter term is sometimes applied to the whole posterior olfactory lobe, though the two parts are said to have different origins (Herrick). This region is separated laterally from the neocortex by a groove, the *rhinal fissure* or *limbic fissure* (*sulcus rhinalis, fissura rhinica, fovea limbica*), while a slight depression, the *incisura rhinica*, bounds the anterior part of the lobe medially (Pls. II., XIV.-XXIV.). The anterior olfactory lobe is probably concerned particularly with the "oral sense", which is simply correlated smell, touch, taste, and muscle sensibility of the snout region, and which is important in feeding reflexes.

The cortex of the anterior olfactory lobe, or praepyriform cortex, differs from the cortex of the pyriform lobe and the neocortex in being thinner and in consisting of only three layers, the *zonal* or *plexiform*, *granular*, and *ganglionic layers* (*laminae zonalis, granularis*, and *ganglion-aris*). The granular layer of the praepyriform cortex is a dense band of cells, which (except at its anterior and posterior extremities) forms a series of longitudinal folds covering the ventral surface of the hemisphere and extends at its medial edge to the ventral part of the septum. From these folds of the granular layer, which serve to increase its area, small groups of cells separate off as the *islands of Calleja* (*ganglia olfactoria*), and certain special nuclei are distinguished in the medial part (nuclei of the medial and lateral olfactory tracts). This large area with the cortical folds and islands is usually called the *tuberculum olfactorium*, but includes also the anterior perforated substance. Both of these are much reduced

in the human brain, only the latter being recognized as a rule.   The
tuberculum olfactorium has connections with the pyriform lobe and the
septum.   Anteriorly, it becomes continuous with the anterior olfactory
nucleus (p. 96).   Laterally and posteriorly, the praepyriform cortex
passes into that of the pyriform lobe, which is distinguished by greater
thickness and by a larger number of cell layers.   The external granular
layer in it is particularly conspicuous, being composed of crowded, deeply-
staining cells, while the subjacent layers are more diffuse.   It not only
receives secondary olfactory fibres, like the praepyriform cortex, but also
is the terminus of many tertiary fibres from the latter area as well as of
axons from other regions.

Closely related to the pyriform lobe in function, and
covered ventrally and laterally by it, is the *amygdaloid
complex* (*amygdala*, *nucleus amygdalae*).   This is a group of
several distinct nuclei which may have various functions and
various origins, but at least some of which—and probably all,
according to Johnston—belong to the olfactory system in
company with the pyriform cortex.   The amygdala certainly
has important somatic functions also, however (p. 107).

The nuclei of this complex are six in number according to Johnston,
who names them topographically.   A rather large mass is the small-
celled *central nucleus*, directly medial to which is a superficial *medial
nucleus* (Pls. XVIII.-XX.).   These are derived from the posterior portion
of a ridge of gray matter (the bed of the stria terminalis—p. 96) belonging
to the primitive olfactory apparatus.   A conspicuous, rounded group of
rather larger cells superficially situated anterior to the medial nucleus is
also a remnant of the latter apparatus.   This is the *nucleus of the lateral
olfactory tract* (*praesubicular area*) (Pl. XX.).   Ventral to the central
nucleus, and pushing partly in between it and the medial nucleus, is the
basal nucleus (Pls. XVIII., XIX.), which is less well developed in the rat,
where it is composed of small cells, than in some other mammals, where
it has distinct large- and small-celled parts.   Dorso-lateral to the basal
and central nuclei is a distinct mass lying between the external capsule
and the ventricular surface, the *lateral nucleus* (Pls. XVIII.-XX.).   The
basal and lateral nuclei are of more recent origin than those previously
mentioned and have been derived from the pyriform cortex by infolding
or immigration of cells along the line of the endorhinal groove.   Finally,
there is a *cortical nucleus* in a superficial position between the medial

nucleus and the endorhinal groove (Pls. XVIII., XIX.). This belongs with the first group, but has been modified by the processes involved in the formation of the newer centres.

Medially, the tuberculum olfactorium (except a small part anteriorly) joins the ventral edge of the *septum*, which forms the medial wall of the anterior part of the lateral ventricle. This structure appears as a fairly thick plate of gray matter penetrated by a large number of medullated fibres, most of which are directed dorso-ventrally. Anteriorly, it rapidly tapers off between the tuberculum olfactorium and the hippo-campus (praecallosal portion—fig. 8) and it is most easily recognized under the corpus callosum. The upper part of the septum extends postero-dorsally between the corpus callosum and the fornix and hippocampal commissure (Fig. 8) and in the human subject this part becomes secondarily separated from the remainder. To it the term septum pellucidum is applied, while the remainder is known as the *subcallosal gyrus* or *paraterminal body* (Pl. XXII.).

Thus the septum as a whole is composed of two parts, the *area prae-commissuralis septi* or *paraterminal body*, and the *pars supraforaminalis* or *pars fimbrialis septi*. According to Johnston, the latter is of pallial origin and is alone entitled to the name of septum (Fig. 8), while the term par-olfactory area may be applied to the remainder. This must not be con-fused with Edinger's lobus parolfactorius, which is the tuberculum ol-factorium.

The myelinated fibres in the septum fall into medial and lateral groups, the former consisting of numerous relatively thick fibres which form a distinct layer on the medial side of the septum, the *bundle of Zuckerkandl* or *fasciculus prae-commissuralis* (*tractus lobo-hippocampalis*, *tractus cortico-olfactorius septi*), while the latter is made up of finer fibres more diffusely arranged. This system comprises several different kinds of fibres, including axons both to and from the septum as well as others which pass right through it. At least some of the fibres arising in this region go to the hypo-

thalamus and others go to the cerebral cortex, while many of those ending in it are tertiary olfactory fibres from the various secondary areas which have just been described. Many of the latter, however, pass on to end in the hippocampus. Ascending fibres from centres lower in the brain also reach the septum. The medial olfactory stria sends many of its fibres into this region.

Connecting the septum with the amygdala and the pyriform cortex is a thick strip of gray matter mingled with a diffuse tract of white fibres, the whole being known as the

Fig. 4

Diagram of some of the principal olfactory pathways in the rat, from Herrick, Introduction to Neurology.

The chief connections of the medial and intermediate olfactory tracts are indicated; those of the lateral olfactory tract are omitted: *c. mam.*, corpus mamillare; *col. forn.*, columna fornicis; *com. ant.*, commissura anterior; *com. hip.*, commissura hippocampi; *com. post.*, commissura posterior; *form. bulb.*, formatio bulbaris; *f. retr.*, fasciculus retroflexus of Meynert; *hab.*, habenula; *h. pc.*, hippocampus praecommissuralis; *h. sc.*, hippocampus supracommissuralis (indusium griseum); *n. ant.*, nucleus anterior thalami; *n. olf. ant.*, nucleus olfactorius anterior; *n. pop.*, nucleus praeopticus (ganglion opticum basale); *S.*, septum; *str. med.*, stria medullaris thalami; *tr. mam. th.*, tractus mamillo-thalamicus (Vicq d'Azyri); *tr. olf. hypth.*, tractus olfacto-hypothalamicus or basal olfactory tract; *tr. olf. tegm.*, tractus olfacto-tegmentalis; *tub. f. dent.*, tuberculum fasciae dentatae (hippocampus postcommissuralis); *tub. olf.*, tuberculum olfactorium.

diagonal band of Broca (Pls. XXI., XXII.). The posterior extremity of this mass of gray matter becomes continuous with the central and medial amygdaloid nuclei. It extends antero-medially and turns up in the posterior part of the septum, mingling with other fibres of the praecommissural system. Most of the fibres of the diagonal band pass right through the septum to end in the hippocampus. The diagonal band also contains fibres connecting the amygdala with the tuberculum olfactorium.

Another connection between the amygdala and the septum is made by one of the bundles which form the *stria terminalis* (*stria seu taenia semicircularis*, *stria cornea*). This is a massive tract which accompanies the caudate nucleus (p. 105)—though largely separated from it in the rat by the internal capsule— in its curving course from the septal region in front of the anterior commissure (vide infra), where the tract appears rather diffuse, round to the amygdaloid complex and is distributed to the various nuclei of the latter and to the neighbouring pyriform cortex. These it connects with other parts of the olfactory apparatus (Pls. XVIII.-XXI.).

Johnston finds the stria terminalis to be made up of five components in the rabbit, man, and other mammals, and Gurdjian has largely confirmed his description for the rat.

(1) The commissural bundle is, in the rat, a distinct bundle of rather fine fibres which can be followed from the nucleus of the lateral olfactory tract through the stria terminalis, forming the most ventral part of its dorsal loop and running into the anterior commissure. It crosses in the most posterior part of the commissure and passes to the nucleus of the lateral olfactory tract on the other side; or, according to Gurdjian, to the cortical olfactory areas in the rat.

(2) The hypothalamic bundle (olfactory projection tract of Cajal) is the largest bundle. It arises from the central and medial amygdaloid nuclei, and anteriorly turns down behind the anterior commissure to run back in the medial forebrain bundle (vide infra). In the rat it ends largely in the praeoptic region.

(3) The infracommissural bundle passes forward under the anterior commissure into the gray matter just lateral to the lateral ventricle, and posteriorly connects with the basal nucleus of the amygdala.

(4) The supracommissural bundle also connects with the basal nucleus, while anteriorly it partly runs into the paraterminal body of the septum and partly turns back under the anterior commissure to join the medial forebrain bundle. The latter portion can be followed into the praeoptic and hypothalamic regions in the rat.

(5) The stria medullaris bundle has already been described (p. 74).

The stria terminalis is accompanied in the reptiles and in mammalian embryos by a ridge of gray matter, the *bed of the stria terminalis*. In adult mammals, this is reduced along the main part of the course of the stria to the condition of a few scattered cells among the fibres of this tract. At the anterior end of the stria, however, there remains a considerable mass of gray matter near the anterior commissure, which is particularly largely developed in the rat (Pl. XXI.). This is continuous with the gray matter surrounding the commissure (the bed of the anterior commissure) and extends forward and downward over the medial surface of the anterior limb of the commissure (p. 97) to merge with the medial part of the head of the caudate nucleus with the nucleus accumbens (p. 106). Thus these latter structures are seen to belong to the olfactory system, of which the bed of the stria terminalis is a part. They are, moreover, both continuous anteriorly with a mass of secondary olfactory cells in the basal wall near the olfactory bulb, which mass has received the name of anterior olfactory nucleus (Fig. 4).[1]

Other fibres connecting the amygdala with several different regions are contained in the rather diffuse *longitudinal amygdalo-pyriform association bundle* (*sagittales Längsbündel, tractus cortico-amygdaloideus*) shown in Pls. XIX. and XX.

A crowded group of large cells situated at the ventral surface immediately in front of the optic chiasma on each side, and extending posteriorly dorsal to the latter, is the *praeoptic nucleus* (*nucleus praeopticus, nucleus magnocellularis praeopticus, ganglion basale opticum*), which is related to the paraterminal body both in its origin and in its connections.

[1]Authorities differ as to the definition of this nucleus. According to Herrick (Jour. Comp. Neur., vol. 37, pp. 317-359) it includes the part mentioned on p. 90 as anterior end of the lateral olfactory gyrus and extends back from the olfactory bulb above the anterior end of the tuberculum olfactorium. A distinct lamina superficial to the anterior end of the lateral olfactory gyrus is the pars externa of the anterior olfactory nucleus of Herrick. See particularly Gurdjian '25 and Obenchain '25. The part marked noa in Pl. XXIII belongs to the caudate nucleus.

From the secondary olfactory areas, tertiary fibres run to the habenula (stria medullaris thalami) and to the hypothalamus (*tractus olfacto-hypothalamicus, basal olfactory tract, basal olfactory projection tract* (Pls. XVII.-XX.), while others descend to the lower parts of the brain. All these tracts together form the large, more or less diffuse *medial forebrain bundle* (Pls. XX., XXI.). The farther pathways from the lower centres have been considered in the previous chapter. A great many of the tertiary olfactory fibres, however, belong to the olfacto-cortical group, which ends in the hippocampus[1] (vide infra).

The olfactory centres of the two sides are, moreover, connected by the *anterior commissure* (*commissura anterior cerebri*), a large structure crossing between the hemispheres in the anterior wall of the telencephalon medium (lamina terminalis). The bundle consists of two parts which are quite distinct, the more anterior being composed of large fibres deeply stained by the Weigert method, while the remainder is made up of smaller, less heavily myelinated fibres which take a paler stain. The anterior part is generally held to be made up largely of secondary olfactory fibres connecting the two olfactory bulbs, while the posterior or temporal portion is chiefly a commissure between the two pyriform lobes.[2] As might be expected, the anterior portion, which is large in the rat and other macrosmatic animals, is very much smaller in the human brain, where also the commissure

[1]Kappers differentiates the cortex of the olfactory lobe (cortex piriformis and praepiriformis), which receives secondary olfactory fibres as *palaeocortex*, and terms the hippocampus, which receives olfactory fibres only of the third and higher orders, *archicortex*. The latter term is frequently applied by other writers to the whole of the olfactory cortex.

The olfacto-cortical fibres from the tuberculum olfactorium (p. 94) reach the hippocampus (and indusium) through the fimbria, the fornix superior, and the striae Lancisii.

[2]A narrow zone of fibres on the lateral aspect of the bulbar portion of the commissure connects the anterior parts of the lateral olfactory areas

as a whole is relatively poorly developed. Between the two parts there is an almost continuous series of fibres connecting the olfactory areas all along the hemisphere (Gurdjian).

The arrangement of the *tertiary olfactory cortex, hippocampus* or *Ammon's horn* (*cornu Ammonis*) is a little difficult to understand at first, and as it is explained by the phylogenetic history of the hemisphere, a brief summary of the latter is introduced here.

The hippocampus is derived from what was originally the dorsal half of the medial wall of the cerebral hemisphere. Ventrally, this region met the dorsal edge of what was to become the septum, while dorsally, it came into contact with the part which was to become the pyriform lobe (Fig. 5). Between it and the last-mentioned part, the neopallium later developed in the dorsal wall of the hemisphere, separating these two olfactory regions. As the neopallium grew in extent longitudinally as well as transversely, it pushed the posterior parts of the hemisphere downwards, so that the originally straight primordium of the hippocampus was bent down posteriorly, curving round until its posterior end pointed antero-ventrally in the temporal region of the hemisphere (Figs. 6, 7). At the same time, the transverse growth of the neopallium forced the primordium of the pyriform lobe down laterally until it reached the ventral position where we have seen it in the rat and finally the ventro-medial location which it occupies in man. The hippocampal area, however, could not be thus displaced and consequently became folded inwards so that most of it lay at the bottom of a deep groove, the hippocampal fissure. It appears in this condition in the marsupials, but in the placental mammals the increasing pressure of the neopallium and the development of the corpus callosum have resulted in the degeneration of the anterior and dorsal part, so that only the posterior part which curves down into the temporal lobe remains well developed (Fig. 8). The remainder is represented only by

of the two hemispheres. There are also commissural and decussating fibres from a pair of small *bed nuclei of the anterior commissure* and the stria terminalis component which is mentioned on p. 95.

Kappers, in his recent text-book, calls the anterior part of this commissure *pars olfactoria* and the posterior part *pars neocorticalis*, maintaining that the latter is made up of neocortical commissural fibres like those of the corpus callosum. He describes four different kinds of fibres in the pars olfactoria (one of these being the commissural bundle of the stria terminalis), but denies that any of these arise in the olfactory bulb.

a very thin band of gray matter, the *indusium* (*indusium griseum, gyrus supracallosus*), accompanied by a few white fibres (*striae longitudinales Lancisii*), which runs along the dorsal surface of the corpus callosum under the edge of the outermost layer of the cerebral cortex. Johnston figures a groove, the fimbrio-dentate fissure, between the indusium and the medial stria of Lancisi in the rat, but the present writer has been unable to recognize this in his specimens.
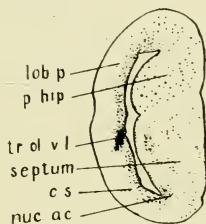
Fig. 5

Transverse section of the left cerebral hemisphere of the frog, from Herrick.

c.s., corpus striatum; *lob. p.*, lobus piriformis; *nuc. ac.*, nucleus accumbens septi; *p. hip.*, primordium hippocampi; *tr. ol. v. l.*, tractus olfactorius ventro-lateralis.

The indusium, or supracallosal hippocampus, is less reduced in the rat than in man, but even here it appears in cross sections as a very small group of cells, which require a special cell stain to demonstrate them clearly (Fig. 9, Pls. XVIII.-XX.). In front of the corpus callosum, there is an unusually large remnant of the hippocampus to be found in the rat, where the typical hippocampal structure is to be seen, though without any involution (Figs. 8, 9). At the genu of the corpus callosum, part of the hippocampal formation extends back ventral to it for a short distance, while the rest is seen to curve round it and become continuous with the indusium. The dorsal band of cells is accompanied by a somewhat dispersed group of fine myelinated fibres, mostly belonging to the olfacto-cortical tract, which form the striae Lancisii.

The postcommissural hippocampus, *i.e.*, the portion behind and below the corpus callosum, is large and well-developed (Fig. 8, Pls. IV., XV.-XX.).

The hippocampal formation is divided into two parts, the *hippocampus proper* and the *fascia dentata* or *gyrus dentatus*

Fig. 6

Diagram of the medial surface of the cerebral hemisphere of the frog, with the primordium hippocampi shaded.   From a sketch by Herrick made with slight modification from a model by Johnston.

(Pls. IV., XV.-XX.).   The hippocampus proper is the larger part, which is folded in at the hippocampal fissure and forms a prominent ridge in the ventricle.   The ventricular surface is covered with a layer of white fibres, the *alveus*, composed of hippocampal projection fibres, and these join a large tract
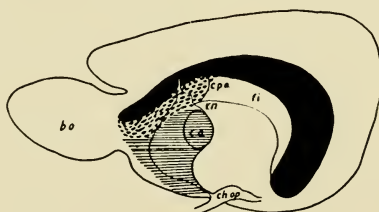
Fig. 7

Diagram of the medial surface of the cerebral hemisphere of a marsupial (opossum), from Johnston; hippocampus solid black; septum shaded, with pallial and basal regions distinguished (see p. 93).

which runs along the side of the hippocampal ridge and is known as the *fimbria*. The stria medialis Lancisii is the reduced fimbria of the degenerated supracallosal part of the hippocampus. The fornix, which has been seen ending in the mamillary body, is the direct continuation of the fimbria.
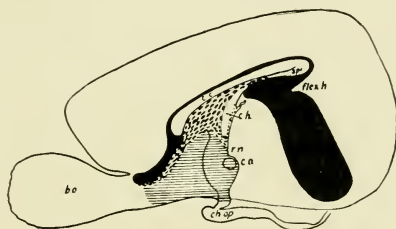
Fig. 8

Diagram of the medial surface of the cerebral hemisphere of the rat, from Johnston; shading as in Fig. 7.
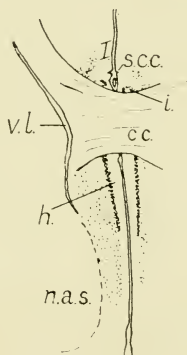
Fig. 9

Middle part of a transverse section of the brain of an albino rat immediately behind the genu of the corpus callosum, stained with a cell stain; *c.c.*, corpus callosum; *h.*, hippocampus (praecallosal portion extending back a short distance under the genu); *i.*, indusium griseum; *n.a.s.*, nucleus accumbens septi; *s.c.c.*, sulcus corporis callosi; *v.l.*, lateral ventricle; *I.*, lamina zonalis of the neocortex.

The hippocampus is composed of three layers of cells, the *molecular, pyramidal*, and *polymorphic*, of which the pyramidal layer stands out clearly on account of the rather crowded arrangement of its perikarya. The dentate gyrus is likewise composed of three layers, in this case *molecular, granular*, and *polymorphic*. It runs along the edge of the hippocampus and is folded around it, the two portions overlapping considerably. The cells of the granular layer are very closely crowded, making it a conspicuous object in sections where they are stained. The functions of the fascia dentata are chiefly reception and local coördination. Most of the axons of the granule cells pass to the hippocampus proper, which gives rise chiefly to commissural and descending projection fibres.

The afferent fibres to the hippocampal formation are divisible into medial and lateral groups. The former arise from the various parts of the secondary olfactory area and the septum and make up a considerable part of the fibre system which has already been noted in the latter structure. They are distributed to the hippocampal cortex in various ways, but chiefly through the fimbria and alveus. The lateral group, or *external hippocampal fibres* (*fibrae hippocampales externae*), arise from both praepyriform and pyriform areas and either join the alveus or run into the surface of the molecular layer of the hippocampus. Non-olfactory fibres enter the hippocampus directly from neighbouring parts of the neopallium.

Efferent fibres from the hippocampus run anteriorly through the fimbria into the fornix. The latter forms a sweeping curve anteriorly (*body of the fornix*), which in the rat is almost absent, as the dorsal end of the hippocampus and the fimbria extend forward practically to the lamina terminalis (Fig. 8) in the position otherwise occupied by the body of the fornix (Pls. XIX.-XXI.). The fornix now turns ventrally into the lamina terminalis, where it passes ventrally and then posteriorly (*column of the fornix*), proceeding back

with a much more gradual curve in the medial part of the thalamus. A large proportion of the fornix fibres (*tractus cortico-mamillaris*) continue backwards in this way until they reach the mamillary body, where, as already observed, many end while a few decussate and pass farther down in the brain stem. In the earlier part of their course, these fibres are accompanied by hippocampal fibres for the habenula (*tractus cortico-habenularis medialis*), which separate off just after the fornix turns backwards, postero-dorsal to the anterior commissure, and pass posteriorly and dorsally in the stria medullaris thalami. This bundle we have seen to accompany the habenular nuclei and end in them on the same and the opposite sides.

The hippocampus also gives rise to a large number of commissural fibres which run to the same region of the other hemisphere, forming the *hippocampal commissure* or *psalterium* (*commissura hippocampi, lyra*). In man, this is a thin plate of transverse fibres crossing between the bodies of the fornix of the two hemispheres and merging at either side into the alveus. In rodents, there is a very large commissure (*ventral hippocampal commissure, commissure of the fimbria, psalterium ventrale*) just behind the ventrally directed columns of the fornix in the lamina terminalis, and this has a thin dorsal extension (*dorsal hippocampal commissure, psalterium dorsale*) which stretches back ventral to the corpus callosum until it reaches the splenium, with which it seems to merge. This extension is thickest in its posterior part, which is really a distinct structure, and which Cajal believes not really to be commissural in character, terming it the *crossed temporo-hippocampal tract*. Some other authors seem to consider the latter portion as part of the splenium, though it is clearly different from the rest of that structure, taking a deeper stain in Weigert preparations (Pl. XXVI.).

The fibres of the ventral hippocampal commissure partly run through a small-celled mass of gray matter lying between it and the columns of the

fornix. This bed of the commissure belongs morphologically to the dorsal part of the septum. Continuous with it, a little mass of cells just where the anterior end of the membranous roof of the third ventricle meets the posterior surface of the commissure has been described in the rat and other forms by Johnston as the *nodulus marginalis*.

Another longitudinal band of hippocampal projection fibres may be seen to separate from the alveus in its postero-dorsal part and to take up a position near the middle line between the corpus callosum and the dorsal hippocampal commissure. There it is joined by small bundles which cross through the corpus callosum from behind and above. This is the *fornix superior*, a structure which is inconspicuous in man, but is very prominent in the rat and in many other mammals (Pls. XIX.-XXI.). This band increases in size as one passes forward to the region of the lamina terminalis, where many of its fibres join the descending columns of the fornix, while others mingle with the praecommissural system in the septum. A much reduced remnant of the fornix superior may be traced some distance farther forward, when it will be found to come from the olfacto-cortical tract (Pls. XXII., XXIII.). The *perforating fibres* which run through the corpus callosum to the fornix superior are derived partly from the indusium, but many come from the region of the cingulum (p. 109), after originating in the interhemispheric cortex (chiefly from its posterior and middle regions in the rat). These, with the fornix superior itself, are frequently called *fornix longus*, a term which seems to have been used in somewhat different ways by different writers. A few fibres of the fornix system, after traversing the septum, join the medial forebrain bundle for the hypothalamus.

A diffuse tract running backwards in the molecular layer of the cortex and mingling with the external hippocampal fibres connects the deeper part of the corresponding layer of the hippocampus with the subsplenial gyrus and the neo-pallium caudal to it (Pls. XV.-XIX., XXVI.).

CHAPTER XIII.

Telencephalon—Non-olfactory Portions.

THE non-olfactory portions of the telencephalon comprise the *basal ganglia* and the *neopallium*. The basal ganglia, according to the usual classification, consist of four centres, the *caudate* and *lentiform nuclei*, the *amygdala*, and the *claustrum*, though the claustrum is really derived from the pallium. The amygdala, moreover, is not really non-olfactory, as we have already seen. The caudate and lentiform nuclei, with the white fibres passing between or through them, make up the *corpus striatum*, in which the amygdala is sometimes included.

In the majority of mammals, including the human species, the caudate and lentiform nuclei are separated by a thick mass of myelinated fibres, the *internal capsule*, which is a direct upward continuation of the pes pedunculi, and which is composed chiefly of ascending and descending axons between the non-olfactory cerebral cortex and lower parts of the brain (projection fibres). In the rat, however, as is found to be the case in many other lower mammals, though usually in a smaller degree, the internal capsule has a more primitive form, being made up of small bundles of fibres scattered through the gray matter, so that there is no sharp division of the latter into two parts (Pls. XIX.-XXIII.). As a matter of fact, the internal capsule never extends far enough forward to separate the two parts completely, and even in man, where there is the greatest separation, the anterior end of the caudate nucleus is continuous with that of the outer part (putamen) of the lentiform nucleus.

The division into caudate and lentiform nuclei (*nucleus*

caudatus and *nucleus lentiformis seu lenticularis*) is not really the fundamental one in the corpus striatum, however, the lentiform nucleus consisting of two parts, the lateral *putamen* and the medial *globus pallidus*, of which the putamen is much more closely related to the caudate nucleus than to the globus pallidus. The putamen and caudate nucleus together form the *neostriatum*, the globus pallidus is the *palaeostriatum*, being much older both phylogenetically and ontogenetically, and the amygdala is called the *archistriatum* according to this terminology.

The caudate nucleus, in animals where it is distinct, has a large anterior portion or *head* (*caput*) and a greatly elongated *tail* (*cauda*) which runs back from the caput dorso-medial to the internal capsule and curves ventrally in the posterior part of the hemisphere. Finally, it turns anteriorly again and ends ventral to the globus pallidus in close topographical relation with the amygdala. In the rat, the bundles of the internal capsule come together posteriorly into a compact mass separating the corpus striatum from the thalamus, but even here there is no definite separation of a caudate nucleus. Ordinary cell stains likewise show no distinction, so the caudate nucleus may be considered to be represented by a considerable anterior portion and a decreasing dorsal, posterior, and postero-ventro-medial portion of the common mass (neostriatum) formed by it and the putamen. At the anterior end of this mass, a large and distinct nucleus projects from it antero-medially under the lateral ventricle into the region of the septum. This *nucleus accumbens septi* (*colliculus striati*)[1] is found in nearly all mammals, as well as in lower vertebrates, but has not yet been recognized in man. The caudate nucleus is made up of two parts which are distinct in the embryo but are indistinguishable in the adult. The medio-ventral portion of the head of the caudate belongs to the olfactory system along with the nucleus accumbens, as

[1]Nucleus parolfactorius lateralis of Johnston.

previously noted (p. 96), while the rest is somatic in its relations, like the remainder of the corpus striatum.

The globus pallidus is a much smaller mass than the neostriatum.[1]   It lies directly medial to the putamen, from which it is distinguished by the fact that it contains a large number of diffuse myelinated fibres. In man and many other animals, it is divided up by thin lamellae of such fibres.

The caudate nucleus and the putamen receive axons through the internal capsule from the thalamus—particularly, probably, from the centre of Luys and the anterior nucleus— while some also come from the red nucleus. Perhaps collaterals from descending cortical fibres also end here. Association fibres connect the striatal nuclei, but are stated to run chiefly from the caudate nucleus to the putamen and from this to the globus pallidus. There are probably descending fibres accompanying the afferent ones mentioned, but most of the descending fibres, at least in higher mammals, seem to come from the globus pallidus through the ansa lenticularis, whence they are distributed to the hypothalamus, the sub- thalamic body, the substantia nigra, and the red nucleus. There is, further, an extensive, diffuse fibre-connection between the lentiform nucleus and the overlying pyriform cortex.

The functions of the corpus striatum are as yet very uncertain. It seems to have an influence upon muscle tone and also to act upon the visceral nervous system.

Related to the parts which we have been considering, is the amygdala (archistriatum of Kappers and his school), which differs from them in receiving several orders of olfactory fibres. Its function, however, is by no means entirely olfactory, as is shown by its considerable development in the dolphin, a totally anosmatic mammal. The amygdaloid complex is to be regarded as a correlation mechanism for

[1]A closely related group of cells, the *basal* or *central nucleus* or *nucleus ansae peduncularis*, is apparently incorporated in the globus pallidus itself in the rat.

many different kinds of afferent impulses, both visceral and somatic.

The remaining mass which is usually classified with the basal nuclei is the *claustrum*, a thin plate of gray matter situated between the putamen and the overlying cortex (insular area). It is separated from the putamen by a rather thin layer of the white matter of the cerebral hemisphere, the *external capsule* (*capsula externa*), and from the cerebral cortex by a considerably thinner layer, the *capsula extrema*. The latter is practically absent in the rat, so that the claustrum cannot readily be distinguished in Weigert sections (Pls. XX.-XXII.). It can be recognized fairly easily, however, in preparations which show the cell-structure, though even there its limits are not very clear, tending to blend with the deepest layer of the adjoining cortex. In the rat, as in some other lower mammals, its ventral edge extends a short distance below the rhinal fissure. The claustrum has been shown by Elliot Smith to be an infolded portion of the cerebral cortex, a source from which the putamen and the greater part of the caudate nucleus have also been derived. Both the fibre-connections and the function of the claustrum are still un-known.

The neopallium, the non-olfactory cerebral cortex with its subjacent white matter, makes up the dorso-medial, the dorsal, and most of the lateral surfaces of the hemisphere of the rat. The early steps of its evolutionary expansion were briefly reviewed in the last chapter. The same process of expansion has continued through the mammalian series to reach its culmination in man. This part of the brain is the physical substratum of all the finer forms of consciousness, all sensory discrimination, and all those processes which we know as mental, intellectual, or psychic.[1]   Experiments with

[1]The physical basis of the emotions, however, is in the thalamus (Head).

rats have proved, however, that a large part of their ability to learn by trial and error has a subcortical basis (Lashley).

The gray matter of the neopallium has all taken up a superficial position, forming the cerebral cortex (*cortex cerebri*), while between this and the lateral ventricle or the basal ganglia, as the case may be, is a thick layer of white matter, the medullary centre of the hemisphere, made up of intrinsic association fibres, interhemispheric commissural fibres, and projection fibres. The proportion of gray matter to white matter is much greater in the rat and other small animals than in man and larger forms generally.[1]

The intrinsic association fibres are of various lengths and serve to connect the different parts of the cerebral cortex of the same hemisphere. The longer ones are largely grouped into rather definite tracts, though these do not show in ordinary sections. The projection fibres include all the ascending and descending fibres which run between the cerebral cortex and lower parts of the brain. These all pass through the internal capsule and spread out at its upper extremity to run directly to the various parts of the cortex, this spreading out of the fibres forming the *corona radiata*.

One prominent tract which is made up of both association and projection fibres connecting with the cortex of the medial surface of the hemisphere above the corpus callosum (inter-hemispheric cortex) and with some related parts in front of it is the *cingulum* (Pls. XVIII.-XXIII.). This is a longitudinal band which curves round the genu of the corpus callosum, runs straight back directly dorsal to the truncus, and extends round the splenium (vide infra). Many of the axons from the interhemispheric cortex bifurcate and send anteriorly- and posteriorly-directed branches through this tract.

The interhemispheric commissural fibres form an immense transverse mass running straight across between the two hemispheres and spreading out in each, the *corpus callosum*.

[1]See de Vries, Anat. Anz., Bd. 37, p. 387.

In a median sagittal section, this structure appears as a rather flat arch, the main part of which is the *body of the corpus callosum* (*truncus corporis callosi*), while the posterior edge shows a rounded thickening, the *splenium*, and the anterior part, also thickened, turns sharply down as the *genu*, tapering rapidly to a point, the *rostrum*, directed postero-ventrally (Pl. XXVI.). In man, the rostrum becomes secondarily connected with the lamina terminalis by a *rostral lamina*, but in the rat, this is absent and the rostrum is not a conspicuous part. The area of the corpus callosum in a median sagittal section, where the corpus itself is cut exactly transversely, gives the only exact indication of its real size. In the adult rat, the area of such a section of the corpus callosum is found to be 3.29% of the computed area of the entire brain, while in man, similar measurements give a ratio of 4.44% (Suitsu). The fibres of the corpus callosum connect with all parts of the neocortex, though all parts are not equally richly supplied with them. Callosal fibres arising from a given area in one hemisphere are distributed to many different parts of the opposite one.

The cortex of the neopallium, or neocortex, is greatly convoluted in man and other large mammals (gyrencephalous species), but in the rat, as in all mammals with small brains the cortex is smooth (lissencephalous). The degree of convolution varies more or less with the gross size of the hemisphere. This is due to the peculiar fact that increase in volume of the neocortex takes place almost entirely by two-dimensional growth—growth in area, while thickness increases relatively little. Thus we find that the average thickness of the cortex of the adult albino rat is fully 1.9 mm. and that of the wild rat about 8% more (Sugita) while that of man is about 3 mm., though the total weight of the human brain is seven hundred times that of the rat brain. The actual thickness of the cortex varies at different points. In a general way, it diminishes from the frontal to the occipital pole, and

from the dorsal aspect to the ventral in the rat. This general statement is probably correct for other mammals also, including man.

The neocortex shows a very definite lamination in its cell-structure, though the laminae are not all so precisely delimited as to bring about complete agreement among the authorities who have studied and enumerated them. Probably the most generally followed scheme is that of Brodmann, who distinguishes six main layers, numbered from the surface inwards as follows:

I.	Lamina zonalis	(Plexiform layer)
II.	Lamina granularis interna.	(Layer of small pyramidal cells)
III.	Lamina pyramidalis.	(Layer of medium and large pyramidal cells)
IV.	Lamina granularis interna.	(Granular layer)
V.	Lamina ganglionaris.	(Inner layer of large pyramidal cells)
VI.	Lamina multiformis.	(Layer of spindle-shaped cells)

These laminae are to be found throughout the mammalia, but in the rat, as in other rodents, layer II. is practically indistinguishable from layer III., so that only five layers are to be recognized (Pl. XXVII.). All the layers superficial to the fifth (*i.e.*, the lamina ganglionaris) probably have receptive and intracortical associative functions, the granular cells giving rise to shorter and the pyramidal cells to longer (inter-regional) association fibres. The two deep layers (V. and VI.), on the other hand, contain the efferent neurons of the cortex and send out projection and commissural fibres, though also containing some short-fibred intra-regional correlation neurons. The outer layers have been shown by Bolton to be the only ones in which there are visible changes corresponding with mental defects in man.

Fig. 10

The appearance of the layers in a typical region of the cortex of the rat may be summed up as follows. The superficial layer, the lamina zonalis (I.), contains only a few scattered glia cells. The lamina pyramidalis (III.) below it is made up of typical, deeply-staining, pyramidal cells, rather closely packed together. Under this layer, the lamina granularis interna (IV.) appears as a band of crowded, deeply-staining, small granules, somewhat resembling glia cells. Beneath this again is the lamina ganglionaris (V.), which contains somewhat scattered, large-sized, deeply-staining pyramids. Finally, the deepest layer consists of a broad zone of polymorphous cells, the lamina multiformis (VI.). These are represented on the left side of Pl. XXVII.

The laminae differ considerably in details of their structure and relative development in different regions of the cerebral cortex, one sometimes even appearing distinctly subdivided, or again one disappearing entirely at certain points. Thus it has been found possible to map out a considerable number of areas in the neocortex, each with a distinct histological structure and, presumably, with a more or less distinct functional significance. Homologous areas can, moreover, be recognized in the various groups of mammals. Further, the principal areas have been shown to have definite differences

Fig. 10. Cortical localization in the wild Norway rat. Diagrams of the lateral, medial and dorsal surfaces, from Fortuyn.

Fortuyn's area.	Brodmann's term.
f, f′	Regio praecentralis.
j, n	Regio parietalis.
w	Regio occipitalis.
k	Regio insularis.
p, x	Regio temporalis.
c	Regio cingularis.
z, z″, z‴	Regio retrosplenialis.
r′, s	Regio hippocampica.
h, h″	Regio olfactoria.

Regio postcentralis is represented in the anterior part of area j.

in vascularity in the rat, as have also the different laminae in a given area, which would seem to indicate differences in functional activity[1] (Pl. XXVII.).

The main areas have been enumerated by Brodmann as follows:[2]

1. Regio postcentralis
2. Regio praecentralis
3. Regio frontalis
4. Regio insularis
5. Regio parietalis
6. Regio temporalis
7. Regio occipitalis
8. Regio cingularis
9. Regio retrosplenialis.

Histological studies reveal a considerably larger number of structurally different areas, however, as may be seen from the accompanying plan of the localization in the cortex of the rat[3] (Fig. 10). In the legend for this illustration, the areas indicated are correlated with the terms of Brodmann. It will be observed that the regio frontalis is not mentioned, this area, though exceedingly large in man, being very small in the rat and being completely hidden at the bottom of the rhinal fissure. It may perhaps be that the area marked d also belongs to this region.

For what is known as to the functions of these areas, the reader is referred to the standard text-books of neurology

[1]Similar differences have been shown between various centres in the brain stem and the cerebellum, and the development of these differences in the young rat has been found to be related temporally to the establishment of functional activity.

[2]Brodmann lists also the olfactory cortex as:

10. Regio hippocampica.
11. Regio olfactoria.

[3]For details of the histological structure in each area shown in Fig. 10, see Fortuyn, Arch. Neur. and Psych., Path. Lab. London County Asylums, vol. VI., 1914, or Sugita, Jour. Comp. Neur., vol. 28, 1917.

and to the special literature. It need only be mentioned here that in a careful effort to show that his area p (temporal area) contains the auditory cortex of the rodent, Fortuyn was unable to obtain any conclusive evidence, though he believes that this is the case. Lashley has plotted the electrically excitable area in the rat, which included approximately areas f and f' and the anterior edges of areas n(?), j(?) and k, and has carried out a large number of experiments which seem to indicate a high degree of transferability of function in the cortex of this animal.

BIBLIOGRAPHY[1]

ADDISON, W. H. F. 1917. The cell-changes in the hypophysis of the albino rat after castration. J. Comp. Neur., vol. 28, pp. 441-463.

BIANCHI, L. (Trans. MACDONALD, J. H.). 1922. The mechanism of the brain and the function of the frontal lobes. Edinburgh. Pp. 348. (Rat, p. 96.)

BREGMANN, L. E. 1915. Neue Untersuchungen zur Kenntnis der Pyramidenbahn. 1. Der Anteil der Pyramide am Rückenmarksquerschnitt bei verschieden Tieren und seine Entwickelung beim Menschen. Anat. Anz., Bd. 48, S. 75-80.

BULLARD, PEARL B. 1912. A comparative study of the three principal regions of the spinal cord in a series of mammals. Am. J. Anat., vol. 14, pp. 73-105.

CAMERON, J. 1904. On the presence and significance of the superior commissure throughout the vertebrata. J. Anat. and Physiol., vol. 38, pp. 275-292.

CRAIGIE, E. HORNE. 1920. On the relative vascularity of various parts of the central nervous system of the albino rat. J. Comp. Neur., vol. 31, pp. 429-464.
    1921. The vascularity of the cerebral cortex of the albino rat. J. Comp. Neur., vol. 33, pp. 193-212.
    1924. Changes in vascularity in the brain stem and

---

[1]A practically complete bibliography for the rat up to the beginning of 1915 has been published by Donaldson in "The Rat" (Memoirs of The Wistar Institute of Anatomy and Biology, No. 6, 1915). The present list contains only the titles of publications referring to the central nervous system of the rat which have appeared since the preparation of Donaldson's bibliography together with a few earlier titles which do not appear in it. It includes not only actual contributions to knowledge of the rat brain, but also the names of some publications containing brief references to or illustrations of this type.

cerebellum of the albino rat between birth and maturity. J. Comp. Neur., vol. 38, pp. 27-48.

1925. Postnatal changes in vascularity in the cerebral cortex of the albino rat. Anat. Rec., vol. 29, p. 354.

Donaldson, H. H. 1916. The relation of myelin to the loss of water in the mammalian nervous system with advancing age. Proc. Nat. Acad. of Sciences, vol. 2, pp. 350-356.

1916a. A preliminary determination of the part played by myelin in reducing the water content of the mammalian nervous system (albino rat). J. Comp. Neur., vol. 26, pp. 443-452.

1916b. A revision of the percentage of water in the brain and in the spinal cord of the albino rat. J. Comp. Neur., vol. 27, pp. 77-115.

1917. Growth changes in the mammalian nervous system. The Harvey Lectures, series 12, 1916-1917, pp. 133-150. Philadelphia.

1918. A comparison of the growth changes in the nervous system of the rat with corresponding changes in the nervous system of man. Proc. Nat. Acad. of Sciences of U.S., vol. 4, pp. 280-283.

1918a. Introduction to the "Comparative studies on the growth of the cerebral cortex," by Dr. Naoki Sugita.

1923. On the effect of captivity or domestication on the brain weight of some mammals. Anat. Rec., vol 25, p. 126.

1923a. On the cranial capacity of the guinea pig—wild and domesticated. Schweizer Archiv fur Neurol. u. Psychiatrie, Bd. 13, S. 206-222.

1923b. On changes in the relative weights of the viscera and other organs from birth to maturity—albino rat. Amer. Jour. Physiol., vol. 67, pp. 1-21.

Donaldson, H. H. and Nagasaka, G. 1918. On the increase in the diameters of nerve-cell bodies and of the

fibres arising from them—during the latter phases of growth (albino rat).   J. Comp. Neur., vol. 29, pp. 529-552.

DUBOIS, EUG.   1923.   Phylogenetic and ontogenetic increase of the volume of the brain in vertebrata.   Kon. Akad. v. Wetens. te Amsterdam, Proc. Sect. Sc., vol. 25, pp. 230-255.

DUNN, ELIZABETH H.   1916.   The size of the medullated axons of the Purkinje cerebellar neurons in the albino rat.   Anat. Rec., vol. 10, p. 196.
1917.   Primary and secondary findings in a series of attempts to transplant cerebral cortex in the albino rat. J. Comp. Neur., vol. 27, pp. 565-582.

EDINGER, L.   1910.   Ueber die Einteilung des Cerebellums. Anat. Anz., Bd. 35, S. 319-323.
1911.   Vorlesungen über den Bau der nervösen Zentralorgane des Menschen und der Tiere.   8te Aufl., Bd. I.

FLATAU-JACOBSOHN.   1899.   Anatomie und vergleichende Anatomie des Centralnervensystems der Säugetiere. Berlin.

FORTUYN, Æ. B. DROOGLEEVER.   1918.   Some remarks about the nervus octavus in three tame rats with inflammation of the internal ear.   Psych. en Neurol. Bladen (Feestbundel Winkler).

FUSE, G.   1919.   Experimentelle Beiträge zur Anatomie des Corpus trapezoides—Pararapheale Durchschneidung des letzteren (Guddensche Methode) an einem Meerschweinchen und rapheale Durchschneidung desselben an einer Ratte (Guddensche Methode).   Arb. a. d. Anat. Inst. d. Kaiserlich-Japanischen Univ. zu Sendai.   Heft 2, S. 191-250.
1919a.   Innerer Aufbau der zentralen akustischen Bahnen.   Arb. a. d. Anat. Inst. d. Kaiserlich-Japanischen Univ. zu Sendai.   Heft 2, S. 275-384.
1920.   Beiträge zur mikroskopischen Anatomie des

Truncus cerebri: einiges vergleichend-anatomisches über das bislang unbekannte resp. nicht genügend berücksichtigte Grau in der Zone zwischen der oberen Olive und der spinalen Quintuswurzel, u. s. w. Arb. a. d. Anat. Inst. d. Kaiserlich-Japanischen Univ. zu Sendai. Heft 4, S. 1-107.

GURDJIAN, E. S. 1925. Olfactory connections in the albino rat, with special reference to the stria medullaris and anterior commissure. J. Comp. Neur., vol. 38, pp. 127-163.

HAMMETT, F. S. 1923. Studies of the thyroid apparatus. XII. The effect of thyro-parathyroidectomy and parathyroidectomy at 100 days of age on the growth of the brain and spinal cord of male and female albino rats. J. Comp. Neur., vol. 35, pp. 313-335.

1924. Studies of the thyroid apparatus. XX. The effect of thyro-parathyroidectomy and parathyroidectomy at 75 days of age on the growth of the brain and spinal cord of male and female albino rats. J. Comp. Neur., vol. 37, pp. 15-30.

HATAI, S. 1915. On the brain-weights of rats descended from the cross between the wild Norway (Mus norvegicus) and the domesticated albino (Mus norvegicus albinus). J. Comp. Neur., vol. 25, pp. 555-566.

1917. Metabolic activity of the nervous system. I. Amount of non-protein nitrogen in the central nervous system of the normal albino rat. J. Comp. Neur., vol. 28, pp. 361-378.

HELD, H. 1890. Der Ursprung des tiefen Markes der Vierhügelregion. Neurol. Centralbl. Bd., 9, S. 481-483.

HERMANÏDES, S. R. und KÖPPEN, M. 1903. Ueber die Furchen und ueber den Bau der Grosshirnrinde bei den Lissencephalen, insbesondere ueber die Lokalisation des motorischen Centrums und der Sehregion. Arch. f. Psychiat., Bd. 37. S. 616-634.

HERRICK, C. JUDSON. 1913. Anatomy of the brain. Wood's
The Reference Handbook of the Medical Sciences, 3rd
edition, vol. 2. New York.
1921. The connections of the vomero-nasal nerve,
accessory olfactory bulb and amygdala in amphibia.
J. Comp. Neur., vol. 33, pp. 213-280. (Rat, pp. 270-
271.)

HOLT, C. M. 1917. Studies on the olfactory bulbs of the
albino rat—in two parts. I. Effect of a defective diet
and of exercise. II. Number of cells in the bulb. J.
Comp. Neur., vol. 27, pp. 201-259.

HOSKINS, E. R. 1916. The growth of the body and organs
of the albino rat as affected by feeding various ductless
glands (thyroid, thymus, hypophysis, and pineal). J.
Exp. Zool., vol. 21, pp. 295-346.

HUNT, H. R. 1924. A Laboratory manual of the anatomy
of the rat. New York. Pp. 123.

INGVAR, S. 1918. Zur Phylo- und Ontogenese des Klein-
hirns nebst einem Versuche zu einheitlicher Erklärung
der zerebellaren Funktion und Lokalisation. Folia
Neurob., Bd. 11, S. 205-502. (The author speaks of
"Rattenkleinhirn" but refers apparently to Mus mus-
culus).

JACKSON, C. M. and CARLETON, RACHEL. 1922. Organ
weights in albino rats with experimental rickets. Proc.
Soc. Exp. Biol. and Med., vol. 20, p. 181.
1923. The effect of experimental rickets upon the
weights of the various organs in albino rats. Am. J.
Physiol., vol. 65, pp. 1-14.

JACKSON, C. M. and STEWART, C. A. 1918. The effects of
underfeeding and refeeding upon the growth of the
various systems and organs of the body. Minnesota
Medicine, vol. 1, pp. 403-414.
1919. Recovery of normal weight in the various organs
of albino rats on refeeding after underfeeding from birth

for various periods. Am. J. of Diseases of Children, vol. 17, pp. 329-352.

1920. The effects of inanition in the young upon the ultimate size of the body and of the various organs in the albino rat. J. Exp. Zool., vol. 30, pp. 97-129.

JOHNSTON, J. B. 1909. The radix mesencephalica trigemini. J. Comp. Neur., vol. 19, pp. 593-644.

1913. The morphology of the septum, hippocampus, and pallial commissures in reptiles and mammals. J. Comp. Neur., vol. 23, pp. 371-478.

1923. Further contributions to the study of the evolution of the forebrain. J. Comp. Neur., vol. 35, pp. 337-481.

KING, HELEN D. 1916. On the postnatal growth of the body and of the central nervous system in albino rats that are undersized at birth. Anat. Rec., vol. 11, pp. 41-52.

KINGERY, H. M. and KINGERY, J. B. 1925. A study of the nervous tissues of albino rats fed on a vitamine-free diet. Anat. Rec., vol. 29, p. 364.

KLEIN, E. and NOBLE SMITH, E. 1880. Atlas of Histology. London. (Rat cerebellum, Pl. XXI, Fig. 7.)

KOCHER, R. A. 1916. The effect of activity on the histological structure of nerve cells. J. Comp. Neur., vol. 26 pp. 241-357.

KOMINE, S. 1919. Metabolic activity of the nervous system. III. On the amount of non-protein nitrogen in the brain of albino rats during twenty-four hours after feeding. J. Comp. Neur., vol. 30, pp. 397-410.

1919a. Metabolic activity of the nervous system. IV. The content of non-protein nitrogen in the brain of the rats kept in a state of emotional and physical excitement for several hours. J. Comp. Neur., vol. 31, pp. 69-82.

KOPPÁNYI, T. and PEARCY, J. F. 1925. Comparative studies on the excitability of the forebrain. Am. J. Phys., vol. 71, pp. 339-343.

Kosaka, K. und Hiraiwa, K. 1914. Zur Anatomie der Sehnervenbahnen und ihren Zentren. Fol. Neurob., Bd. 9, S. 367-389.

Lashley, K. S. 1920. Studies of cerebral function in learning. Psychobiology, vol. 2, pp. 55-135.
1921. Studies of cerebral function in learning. II. The effects of long continued practice upon cerebral localization. J. Comp. Psychol., vol. 1, pp. 453-468.
1921a. Studies of cerebral function in learning. III. The motor areas. Brain, vol. 44, pp. 255-285.
1922. Studies of cerebral function in learning. IV. Vicarious function after destruction of the visual areas. Am. J. Physiol., vol. 59, pp. 44-67.

Lashley, K. S. and Franz, S. I. 1917. The effects of cerebral destruction upon habit-formation and -retention in the albino rat. Psychobiology, vol. 1, pp. 71-139.

Löwy, R. 1910. Zur Frage der superfiziellen Körnerschichte und Markscheidenbildung des Kleinhirns. Ihre Beziehungen zum Lokalisationsproblem und zur Gefähigkeit. Arb. a. d. Neurol. Inst. a. d. Wiener Universität, Bd. 18, S. 251-293. Rat, S. 263-264.

Lotheissen, G. 1894. Ueber die Stria medullaris Thalami optici. Anat. Hefte, Bd. 4, S. 225-259.

MacArthur, C. G. and Jones, O. C. 1917. Some factors influencing the respiration of ground nervous tissue. J. Biol. Chem., vol. 32, pp. 259-274. Rat, table X.

Macklin, C. C. and Macklin, Madge T. 1919. Brain repair in the rat vitally stained with trypan blue. Anat. Rec., vol. 6, pp. 8-10.
1920. A study of brain repair in the rat by use of trypan blue, with special reference to vital staining of the macrophages. Arch. Neur., and Psychiat., vol. 3, pp. 353-394.

Meyersohn, F. 1913. Die Dicke der spinalen Trigeminuswurzel bei verschiedenen Säugern. Fol. Neurob., Bd. 7, S. 217-220.

MURPHY, J. B. and STURM, ERNEST. 1923. Conditions determining the transplantability of tissues in the brain. J. Exp. Med., vol. 38, pp. 183-198.

NICHOLSON, F. M. 1923. The changes in the amount and distribution of the iron-containing proteins of nerve cells following injury to their axons. J. Comp. Neur., vol. 36, pp. 37-87.

NITTONO, K. 1923. On bilateral effects from the unilateral section of branches of the nervus trigeminus in the albino rat. J. Comp. Neur., vol. 35, pp. 133-161.

OBENCHAIN, JEANNETTE B. 1925. The brains of the South American marsupials Caenolestes and Orolestes. Field Mus. of Nat. Hist., Zool. Series, vol. 14, pp. 175-232 (Rat p. 193).

PAPEZ, J. W. 1923. The mamillary peduncle, Marchi method. Anat. Rec., vol. 25, p. 146.
1923a. The thalamic end of the medial lemniscus, Marchi method. Anat. Rec., vol. 25, p. 146.
1923b. The rubrospinal tract, Marchi method. Anat. Rec., vol. 25, p. 147.

PEKELSKÝ, A. 1922. Über die Kerne der Raphe und der benachbarten Anteile der retikulierten Substanz. I. Teil: Säugetiere. Arb. a. d. Neurol. Inst. a. d. Wiener Universität. Bd. 23, S. 21-73. (See footnote, p. 51.)

PLANT, J. S. 1919. Factors influencing the behaviour of the brain of the albino rat in Müllers fluid. J. Comp. Neur., vol. 30, pp. 411-422.

STEWART, C. A. 1916. Growth of the body and of the various organs of young albino rats after inanition for various periods. Biol. Bul., vol. 31, pp. 16-51.
1918. Weights of various parts of the brain in normal and underfed albino rats at different ages. Anat. Rec., vol. 14, p. 51.
1918a. Weights of various parts of the brain in normal and underfed albino rats at different ages. J. Comp. Neur., vol. 29, pp. 511-528.

1919. Changes in the weights of the various parts, systems, and organs in albino rats kept at birth weight by underfeeding for various periods. Am. J. Physiol., vol. 48, pp. 67-78.

SUGITA, N.   1917.   Comparative studies on the growth of the cerebral cortex.   I.   On the changes in the size and shape of the cerebrum during the postnatal growth of the brain.   Albino rat.   J. Comp. Neur., vol. 28, pp. 495-510.

1917a.   Comparative studies on the growth of the cerebral cortex.   II.   On the increase in the thickness of the cerebral cortex during the postnatal growth of the brain. Albino rat.   J. Comp. Neur., vol. 28, pp. 511-591.

1918.   Comparative studies on the growth of the cerebral cortex.   III.   On the size and shape of the cerebrum in the Norway rat (Mus norvegicus) and a comparison of these with the corresponding characters in the albino rat.   J. Comp. Neur., vol. 29, pp. 1-9.

1918a.   Comparative studies on the growth of the cerebral cortex.   IV.   On the thickness of the cerebral cortex of the Norway rat (Mus norvegicus) and comparison of the same with the cortical thickness in the albino rat.   J. Comp. Neur., vol. 29, pp. 11-39.

1918b.   Comparative studies on the growth of the cerebral cortex.   V.   Part I.   On the area of the cortex and on the number of cells in a unit volume, measured on the frontal and sagittal sections of the albino rat brain, together with the changes in these characters according to the growth of the brain.   Part II.   On the area of the cortex and on the number of cells in a unit volume, measured on the frontal and sagittal sections of the brain of the Norway rat (Mus norvegicus), compared with the corresponding data for the albino rat.   J. Comp. Neur., vol. 29, pp. 61-117.

1918c.   Comparative studies on the growth of the

cerebral cortex. VI. Part I. On the increase in size and on the developmental changes of some nerve cells in the cerebral cortex of the albino rat during the growth of the brain. Part II. On the increase in size of some nerve cells in the cerebral cortex of the Norway rat (Mus norvegicus), compared with the corresponding changes in the albino rat. J. Comp. Neur., vol. 29, pp. 119-162.

1918*d*. Comparative studies on the growth of the cerebral cortex. VII. On the influence of starvation at an early age upon the development of the cerebral cortex. Albino rat. J. Comp. Neur., vol. 29, pp. 177-240.

1918*e*. Comparative studies on the growth of the cerebral cortex. VIII. General review of data for the thickness of the cerebral cortex and the size of the cortical cells in several mammals, together with some postnatal growth changes in these structures. J. Comp. Neur., vol. 29, pp. 241-278.

SUITSU, N. 1920. Comparative studies on the growth of the corpus callosum. I. On the area of the corpus callosum, measured on the sagittal section of the albino rat brain. J. Comp. Neur., vol. 32, pp. 35-60.

TILNEY, F. and CASAMAJOR, L. 1917. The development of the hemal channels in the central nervous system of the albino rat. Anat. Rec., vol. 11, pp. 425-428.

TILNEY, F. and RILEY, H. A. 1921. The form and functions of the central nervous system. New York. Rat: pp. 27, 31, 32, 34, 35, 43, 46, 47.

WARREN, J. 1917. The development of the paraphysis and pineal region in mammalia. J. Comp. Neur., vol. 28, pp. 75-135.

ZUCKERKANDL, E. 1909. Zur Entwicklung des Balkens. Arb. a. d. Neurol. Inst. Bd. 17, S. 373-409.

APPENDIX.

PREPARATION OF SECTIONS—METHOD OF WEIGERT.

WHILE the Weigert technique is a standard histological method, there are many modifications of it, with some of which the brain of the rat is sometimes rather refractory. The writer has usually obtained satisfactory results by the following simple form of the method.

The brain is removed from the skull as soon as possible after death and is at once immersed in Müller's fluid (potassium bichromate, 2.5 gm.; sodium sulphate, 1 gm.; distilled water, 100 c.c.). This solution is renewed two or three times during the first week, after which the material is left undisturbed for two months or more, being kept in the dark during this time. The tissue is then washed for a few hours in distilled water and passed into 50% alcohol for a few hours more, after which it is transferred to 70% alcohol, where it may remain for from twenty-four hours to several weeks. It is next kept for twenty-four hours in each of 80%, 95%, and absolute alcohol successively, and passed through cedar oil to paraffin.

Serial sections 15μ-20μ thick are mounted on slides by the ordinary water-albumin method. The paraffin is now washed out of the sections by immersing the slide in xylol, from which it is transferred to absolute alcohol. The slide is next flooded with thin celloidin (0.5%), which is drained off and allowed to dry in the air for a few minutes, and after this the slide is passed rapidly down through a graded series of alcohols to distilled water.

The slides are placed upside down (supported on small slips of glass) in a half-saturated solution of copper acetate

which is kept at a temperature somewhere near 35° C., and remain there over night. After rinsing in distilled water they are transferred to Weigert's haematoxylin (10 c.c. 10% haematoxylin in absolute alcohol+90 c.c. distilled water+ 1 c.c. saturated solution of lithium carbonate), again upside down, in which they are kept for 4-6 hours. Following another rinsing, the sections, which are now deep blue or blue-black, are subjected to the action of Weigert's decolorizer, a fluid composed of equal parts of a 2% solution of borax and a 2.5% solution of potassium ferricyanide. This mixture is used freely until the desired differentiation is obtained, which may be in a short time or may not be for several hours.

The differentiating fluid of Pal (equal parts of 1% oxalic acid and 1% potassium sulphite solutions used after a brief immersion in 0.25% potassium permanganate) is very much more rapid and may give more brilliant results, but is less easily controlled in its action.

The sections are finally washed in running water for twenty-four hours and mounted in Canada balsam.

Suitsu recommends as particularly suitable for the rat brain a modification of the very similar Kultschitzky technique, the description of which may be found in his paper in the Journal of Comparative Neurology, vol. 32, pp. 36-37.

Plate I.   Dorsal view of the brain of an adult albino rat four times natural size.

bo, olfactory bulb; cer. cerebral hemisphere; ch, cerebellar hemi-sphere; ci, posterior colliculus; e, pineal body; pf, paraflocculus; py, pyramis; slp, dorso-lateral groove; smp, dorsal median groove; s1, first cervical spinal nerve, dorsal root; s2, second cervical spinal nerve, dorsal root; u, uvula; vr, vermis.

PLATE I
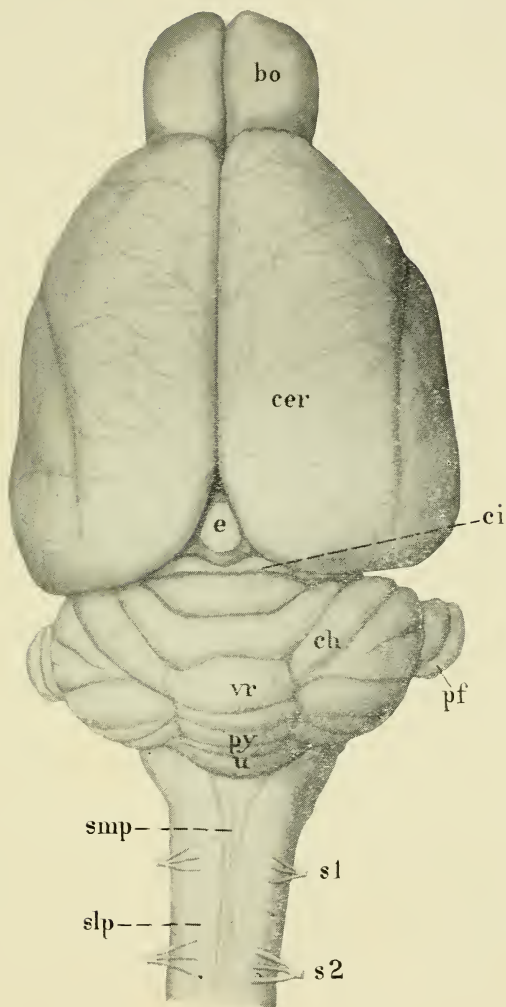
Plate II. Ventral view of the brain of an adult albino rat four times natural size. The representation of the nerve roots is somewhat diagrammatic.

bo, olfactory bulb; cho, optic chiasma; cma, mamillary body; ct, trapezoid body; frh, rhinal fissure; i, infundibulum; lp, pyriform lobe; nc, neopallium; p, pyramid; pf, paraflocculus; po, pons; pp, basis (pes) pedunculi cerebri; s1, first cervical spinal nerve, ventral root; tc, tuber cinereum; to, tuberculum olfactorium; trol, olfactory tract; III., oculomotor nerve; IV., trochlear nerve; V., trigeminal nerve (large sensory and small motor portions); VI., abducent nerve; VII., facial nerve; VIII., auditory nerve; IX.+X., glossopharyngeal and vagus nerves; XI., spinal accessory nerve; XII., hypoglossal nerve.

PLATE II
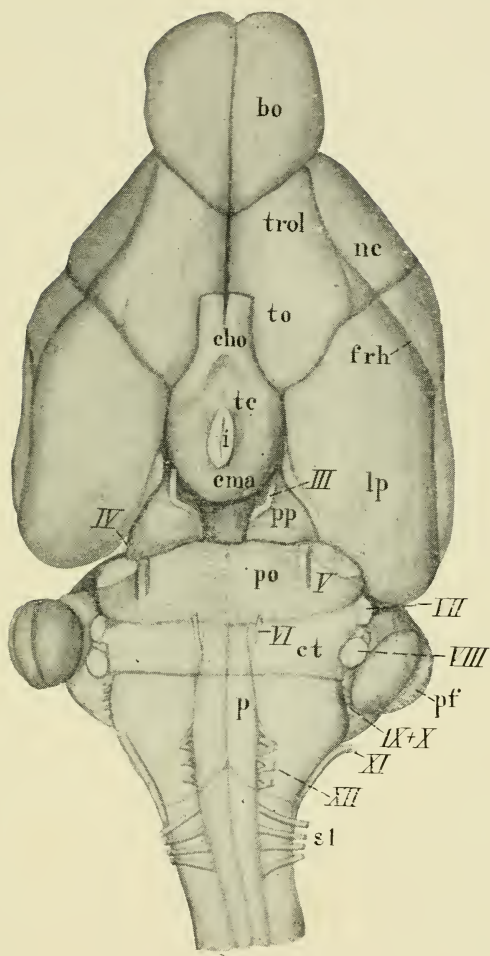
Plate III.   Dorsal view of the brain of an adult albino rat with the cere-
bellum and much of the cerebral hemispheres removed, $\times$ 4.

bc, brachium conjunctivum; bo, olfactory bulb; bpo, brachium
pontis; cc, corpus callosum; ci, posterior colliculus; cl, clava; cr,
restiform body; cst, corpus striatum; csu, anterior colliculus; dc,
tuberculum acusticum; ev, vestibular area (trigonum acustici); f,
facial colliculus; fc, fasciculus cuneatus; fi, fovea inferior; fim,
fimbria; fsu, fovea superior; ft, funiculus teres; gl, lateral geniculate
body; gm, medial geniculate body; nc, cerebral cortex (neocortex);
o, obex; s, septum; sm, stria medullaris thalami running along the
habenula into the habenular commissure; st, stria terminalis; th,
thalamus; tv, taenia ventriculi (line of attachment of posterior
medullary velum); vc, ventral cochlear nucleus; V., trigeminal nerve;
VIII., auditory nerve.

PLATE III
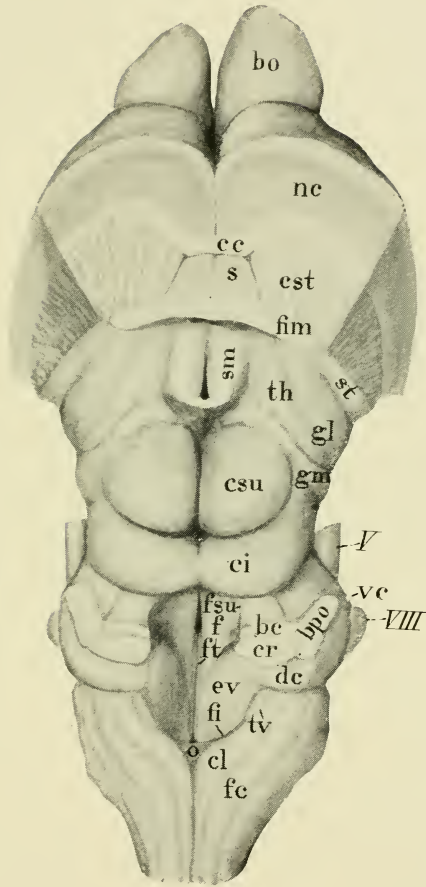
Plate IV. Medial view of the right cerebral hemisphere of an albino rat with most of the thalamus cut away so as to expose the hippocampal formation, × 4.

bo, olfactory bulb; ca, anterior commissure in lamina terminalis; cc, corpus callosum; chd, dorsal part of hippocampal commissure; chv, large ventral part of hippocampal commissure or commissura fimbriae; co, optic chiasma; fac, fasciola cinerea; fch, fissura chorioidea; fd, fascia dentata; fh, hippocampal fissure; fim, fimbria; gs, gyrus subsplenialis; gsc, gyrus supracallosus; h, hippocampus proper covered by white fibres connecting with the fimbria; s, septum; tfd, tuberculum fasciae dentatae; th, cut surface of thalamus.

PLATE IV
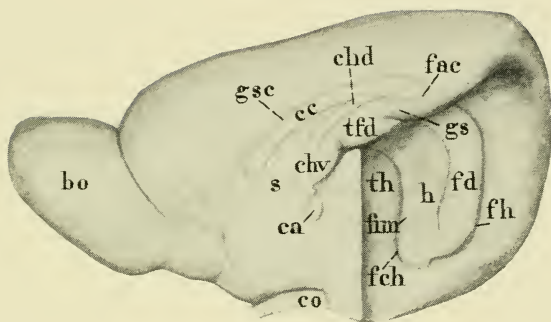
Plate V. Outline drawings of transverse sections through alternate segments (except in the caudal region) of the spinal cord of an albino rat, $\times$ 6.25.

df, dorsal funiculus; l, tract of Lissauer; lf, lateral funiculus; p, pyramidal (cortico-spinal) tract; sr, gelatinous substance of Rolando; vf, ventral funiculus.

PLATE V

C I.

C III.
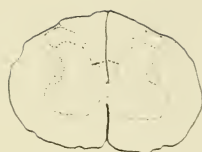
C V.

C VII.

T I.

T III.

T V.

T VII.

T IX.

T XI.

T XIII.

L II.

L IV.

L VI.

S II.

S IV.

C.

Plate VI.   c, central canal;   dp, decussation of the pyramidal tract; fc, fasciculus cuneatus;   fr, reticular formation;   fs, lower end of fasciculus solitarius;   nfl, nucleus funiculi lateralis;   ng, nucleus gracilis;   nXI, nucleus of nerve XI.;   nXII, nucleus of nerve XII.; p, pyramidal tract;   sr, gelatinous substance of Rolando;   XI., nerve XI.;   XII., root of nerve XII.

Plates VI.-XXV.   THE MAGNIFICATION IN PLATES VI.-XXV. INCLUSIVE IS 12.5.   THESE ARE TRANSVERSE SECTIONS THROUGH THE BRAIN OF AN ADULT ALBINO RAT STAINED BY THE METHOD OF WEIGERT.   THE LEVELS OF THE SECTIONS ARE INDICATED IN PLATE XXVIII.

PLATE VI
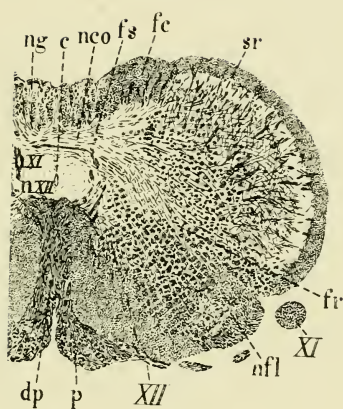
Plate VII. ch, cerebellar hemisphere; dl, decussation of the lemniscus; fai, internal arcuate fibres; flm, medial longitudinal bundle; fra, formatio reticularis alba; frg, formatio reticularis grisea; fs, fasciculus solitarius; ncu, cuneate nucleus; nfl, nucleus of lateral funiculus; nfs, nucleus of fasciculus solitarius; ng, gracile nucleus; nsV, spinal V. nucleus; nX., dorsal motor vagus nucleus; nXII., hypoglossal nucleus; od, dorsal accessory olivary nucleus; oi, inferior olivary nucleus; om, medial accessory olivary nucleus; p, pyramidal tract; r, nucleus of Roller; rsV., spinal V, root; tt, tecto-spinal tract; ug, granular layer of cortex of uvula of cerebellum; um, molecular layer of cortex of uvula of cerebellum; XII., root of hypoglossal nerve.
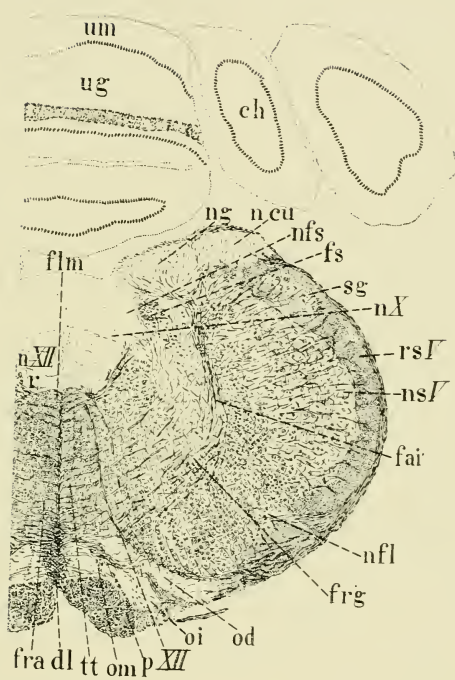
PLATE VII

Plate VIII. fs, fasciculus solitarius; lm, medial lemniscus; n, nodulus of cerebellum; na, nucleus ambiguus; ncu, cuneate nucleus; nfs, nucleus of fasciculus solitarius; ng, gracile nucleus; nlr, lateral nucleus of reticular formation; np, nucleus parasolitarius; ns, nucleus inter-calatus of Staderini; nsV., spinal V. nucleus; nvr, ventral nucleus of reticular formation; nX., dorsal motor vagus nucleus; nXII., hypo-glossal nucleus; od, dorsal accessory olivary nucleus; oi, inferior olivary nucleus; om, medial accessory nucleus; p. pyramidal tract; py, pyramis of cerebellum; rsV., spinal V. root; tsd, dorsal spino-cerebellar tract; tsv, ventral spino-cerebellar tract; u, uvula of cerebellum; ve, fourth ventricle; VIII.c, chief vestibular nucleus; VIII.d, descending vestibular root and nucleus; XII., root of the hypoglossal nerve.

PLATE VIII
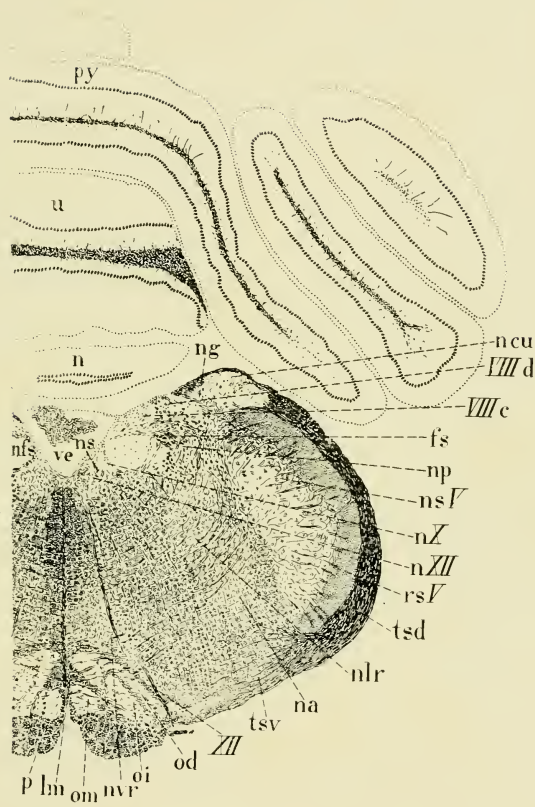
Plate IX.   cr, restiform body; ct, trapezoid body; d, dentate nucleus;
    dc, dorsal cochlear nucleus; dt, nucleus of Deiters; fl, flocculus;
    flm, medial longitudinal bundle; fs, fasciculus solitarius and its
    nucleus; lm, medial lemniscus; me, lobus medius; n, nodulus; ncr,
    nucleus of restiform body; ncvm, caudal ventro-medial nucleus of
    spinal V. root; ne, nucleus emboliformis; nsV, spinal V. nucleus;
    nVII., motor facial nucleus; nvr, ventral nucleus of reticular forma-
    tion; p, pyramidal tract; pf, paraflocculus; rsV., spinal V. root;
    sa, stria medullaris acustica; t, nucleus tecti; tt, tecto-spinal tract;
    vc, ventral cochlear nucleus; VII., fascicles of motor root of facial
    nerve; VIII.c, chief vestibular nucleus.

PLATE IX
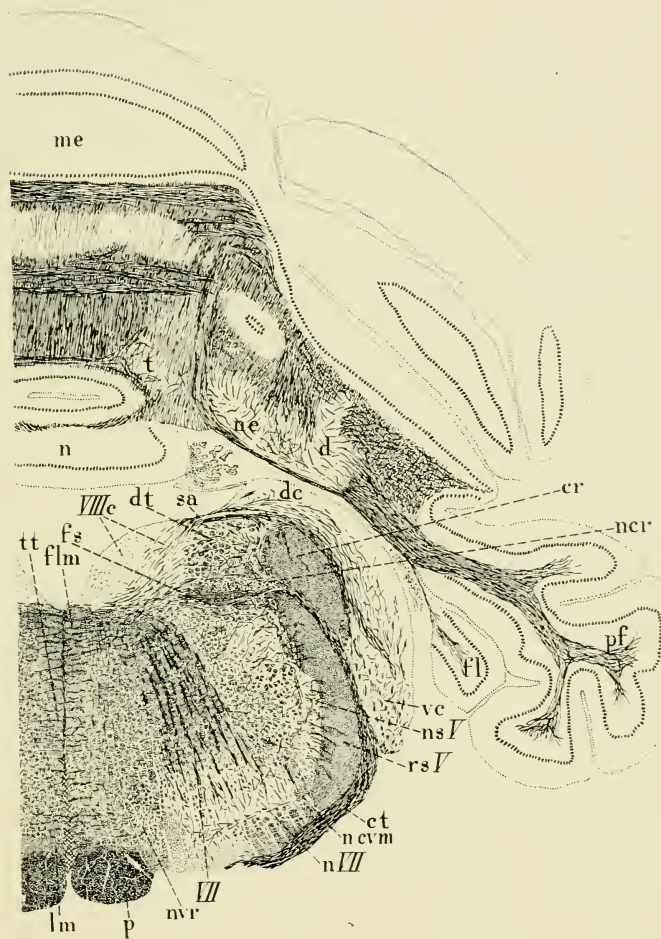
Plate X. b, nucleus of Bechterew; cr, restiform body; ct, trapezoid body; dct, decussation of trapezoid body; dt, nucleus of Deiters; fl, flocculus; flm, medial longitudinal bundle; fo, fibres from superior olivary nucleus to nucleus abducens, etc.; fv, vestibulo-cerebellar fibres; g, nucleus globosus; gVII., genu of motor root of facial nerve; lm, medial lemniscus; npe, nucleus praeolivaris externus; npi, nucleus praeolivaris internus; nsV., spinal V. nucleus; nt, nucleus of trapezoid body; nVI., nucleus of abducent nerve; os, superior olivary nucleus; osa, accessory superior olivary nucleus and its dorso-medial cell group; p, pyramidal tract; pf, paraflocculus; rsV., spinal V. root; tr, rubro-spinal tract; tt, tecto-spinal tract; vc, ventral cochlear nucleus; VI., root fibres of abducent nerve; VII., emerging motor root of facial nerve; VIII.c, chief vestibular nucleus; vs, secondary vestibular fibres.

PLATE X
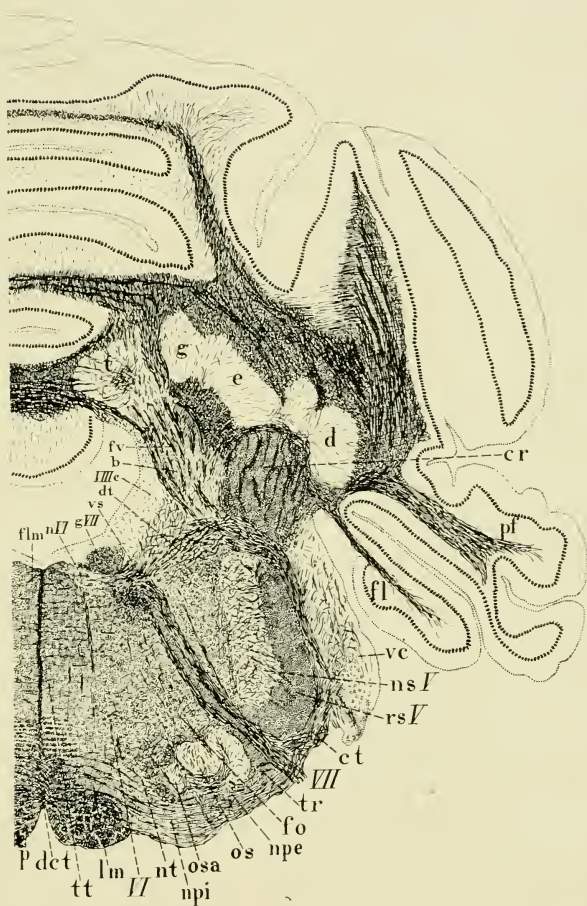
Plate XI. bc, brachium conjunctivum; cr, restiform body; ct, trapezoid body; dct, decussation of trapezoid body; flm, medial longitudinal bundle; fls, dorsal longitudinal bundle of Schütz; la, lobulus ansiformis; lc, locus coeruleus; ll, lateral lemniscus; lm, medial lemniscus; ls, lobulus simplex; 1 I-4, lobules of lobus anterior; ncV., chief sensory nucleus of the V. nerve; nmes, mesencephalic nucleus of the V. nerve with fibres of the mesencephalic root running ventro-lateral from it; nmV., motor nucleus of the V. nerve; novm, anterior cells of oral ventro-medial nucleus of spinal V. root; npi, nucleus prae-olivaris internus; nt, nuclei of the trapezoid body; os, superior olivary nucleus; osa, accessory superior olivary nucleus; p, pyramidal tract; rmV., motor root of V. nerve; rsV., beginning of spinal root of V. nerve; tr, rubro-spinal tract; tsv, ventral spino-cerebellar tract; tsvd, descending part of ventral spino-cerebellar tract accompanying brachium conjunctivum into cerebellum, with fibres of cerebello-bulbar tract (of Russel) under it; vc, ventral cochlear nucleus; vma, anterior medullary velum; VII., anterior part of emerging motor facial root.

PLATE XI
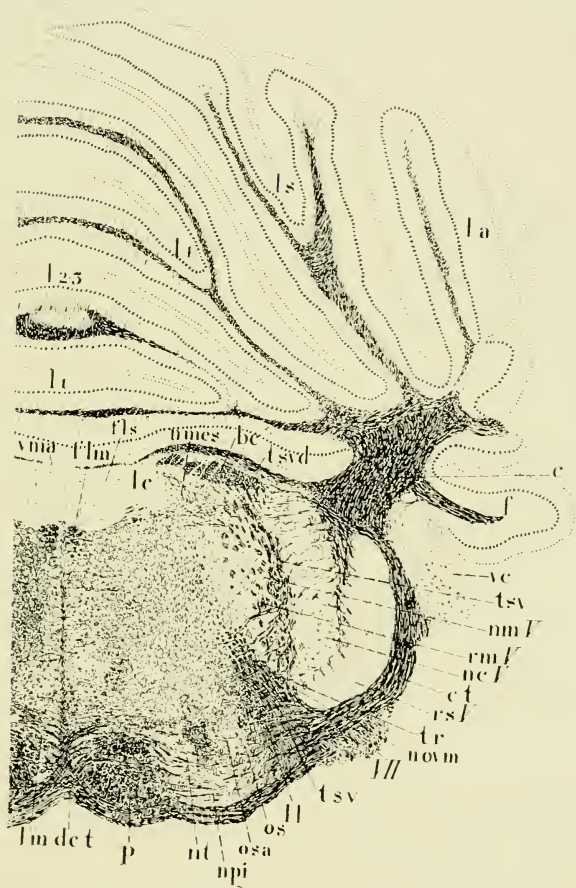
Plate XII. bc, brachium conjunctivum; bi, brachium of posterior colliculus; bpo, brachium pontis; cer, occipital pole of cerebral hemisphere; ci, posterior colliculus; cp, secondary fibres from dorsal nucleus of lateral lemniscus, many of which cross in the *commissure of Probst;* ll, lateral lemniscus with cells of its dorsal nucleus between its fascicles; lm, medial lemniscus; npo, nucleus pontis; nr, nucleus of the raphe; ntd, dorsal tegmental nucleus; ntv, ventral tegmental nucleus; p, pyramidal tract; po, pons; rmes, mesencephalic V. root; rmV., motor V. root; rsV., sensory V. root; tg, mamillo-tegmental tract; tpo, tecto-pontine tract; tt, tecto-spinal tract; IV., root of trochlear nerve.

PLATE XII

ci

cer

bi

r mes

ll

ntd

cp

tg

ntv

ll

be

b po

t po

rm l

p

r s l

tt

npo po ur lm
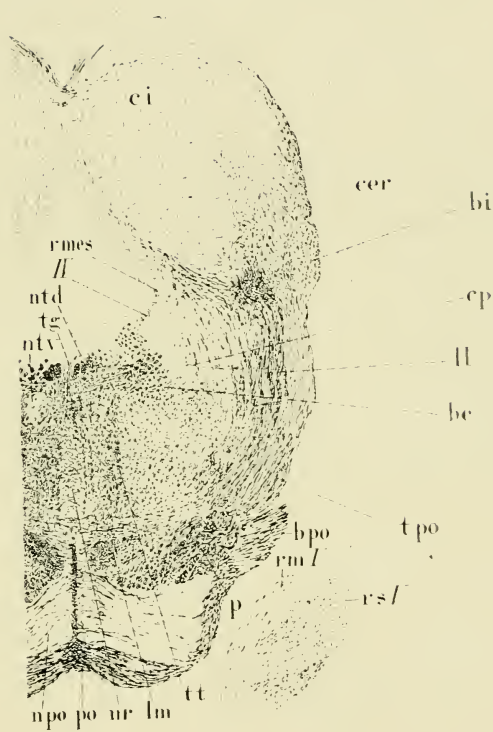
Plate XIII. as, aqueduct of Sylvius; bi, brachium of posterior colliculus; cer, occipital portion of cerebral hemisphere; cg, central gray matter; ci, nucleus of posterior colliculus; dbc, decussation of brachium conjunctivum; ddt, dorsal tegmental decussation (Meynert); dvt, ventral tegmental decussation (Forel); flm, medial longitudinal bundle; lg, laminated gray matter of tectum penetrated by commissure of posterior colliculi; ll, lateral lemniscus; lm, medial lemniscus; ndr, dorsal nucleus of the raphe; ni, interpeduncular nucleus; nIV., nucleus of the trochlear nerve; npo, nuclei of the pons; p, pyramidal tract; po, pons; rmes, mesencephalic V. root; sp, stratum profundum; tg, mamillo-tegmental tract; tr, rubro-spinal tract; tt, tecto-spinal tract; tti, tegmental tract of interpeduncular nucleus.

Plate XIII
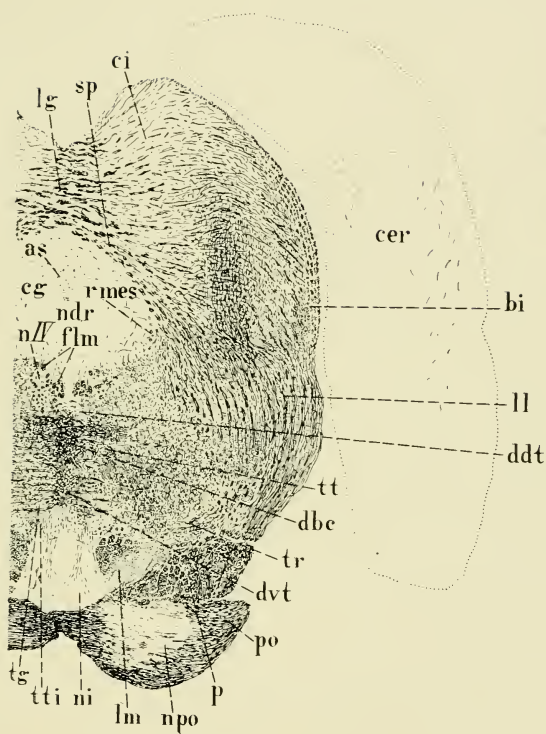
Plate XIV.   bi, brachium of posterior colliculus; bs, brachium of anterior colliculus (optic tract); cg, central gray matter; dvt, ventral tegmental decussation with dorsal tegmental decussation dorsal to it; ew, nucleus of Edinger-Westphal; fm, fasciculus retroflexus (of Meynert); frh, rhinal fissure; ll, lateral lemniscus; lm, medial lemniscus; nc, neocortex; ni, interpeduncular nucleus; nIII., nucleus of oculomotor nerve; nrd, dorso-lateral portion of red nucleus; nrm, magnocellular portion of red nucleus; nrv, ventro-lateral portion of red nucleus; pm, peduncle of the mamillary body; pp, basis pedunculi; pyc, pyriform cortex; rm, fountain radiation of Meynert; rmes, mesencephalic V. root; sg, stratum griseum of anterior colliculus; sl, stratum lemnisci of anterior colliculus; sn, substantia nigra; soa, optic layer of stratum opticum of anterior colliculus; sob, non-optic layer of stratum opticum of anterior colliculus; sp, stratum profundum; sz, stratum zonale; ta, tapetum (a distinct layer of fibres from the corpus callosum); tg, mamillo-tegmental tract; vl, lateral ventricle; w, layer of white matter superficial to tapetum; III., oculomotor nerve root.

PLATE XIV

nc

sg sz

soa

sob
sl
sp

cg   rmes

ew
nⅢ

w

ta

bs

bi

ll

rm

vl

frh

mi

tg

dvt fm nrm

pm

lm pp sn

Ⅲ

nrd

nrv

py c
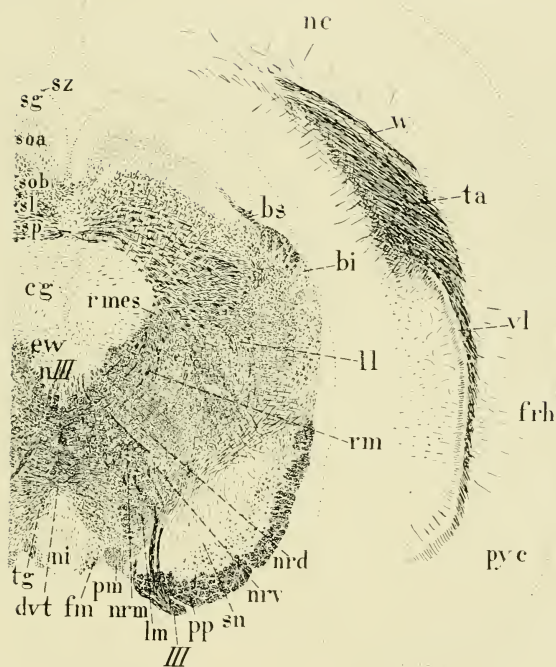
Plate XV. bi, brachium of posterior colliculus; bs, brachium of anterior colliculus; cf, column of the fornix; ds, supramamillary decussation; fd, fascia dentata; fh, hippocampal fissure; fhe, external hippocampal fibres; fhs, fasciculus hippocampo-subsplenialis; flm, medial longitudinal bundle; fm, fasciculus retroflexus; frh, rhinal fissure; gm, medial geniculate body; i, posterior extension of cavity of infundibulum; lm, medial lemniscus; ml, lateral nucleus of mamillary body; mm, medial nucleus of mamillary body; nc, neocortex; nda, nucleus of Darkschewitsch; nic, interstitial nucleus of Cajal; npt, nucleus of transverse peduncular tract; pm, peduncle of mamillary body; pp, basis pedunculi; pyc, pyriform cortex; sg, stratum griseum of anterior colliculus; sl, stratum lemnisci of anterior colliculus; sn, substantia nigra; soa, optic layer of stratum opticum; sob, non-optic layer of stratum opticum; sp, stratum profundum; sz, stratum zonale; ta, tapetum; tg, mamillo-tegmental tract; tpt, transverse peduncular tract; vd'a, mamillo-thalamic tract; vl, lateral ventricle; w, layer of white matter superficial to tapetum.

PLATE XV

Plate XVI.   as, aqueduct of Sylvius; bs, brachium of anterior colliculus; cf, column of the fornix; cg, central gray matter; cpt, posterior commissure; dvt, ventral tegmental decussation; fd, fascia dentata; fh, hippocampal fissure; fhe, external hippocampal fibres; fhs, fasciculus hippocampo-subsplenialis; fm, fasciculus retroflexus; frh, rhinal fissure; gm, medial geniculate body; h, hippocampus; i, infundibulum; lm, medial lemniscus; nc, neocortex; npr, posterior nucleus of thalamus; pp, basis pedunculi; pyc, pyriform cortex; sg, stratum griseum of anterior colliculus; sn, substantia nigra; soa, optic layer of stratum opticum; sob, non-optic layer of stratum opticum; sz, stratum zonale; tc, tuber cinereum; tg, mamillo-tegmental tract; vd'a, mamillo-thalamic tract; vl, lateral ventricle; vt, third ventricle.

Plate XVI

Labels on figure: sz, sg, soa, sob, c pt, a s, c g, fm, tg, dvt, vda, vt, tc, i, i, cf, lm, sn, pp, fhs, fh, fhe, bs, fd, npr, gm, h, vl, nc, frh, pyc
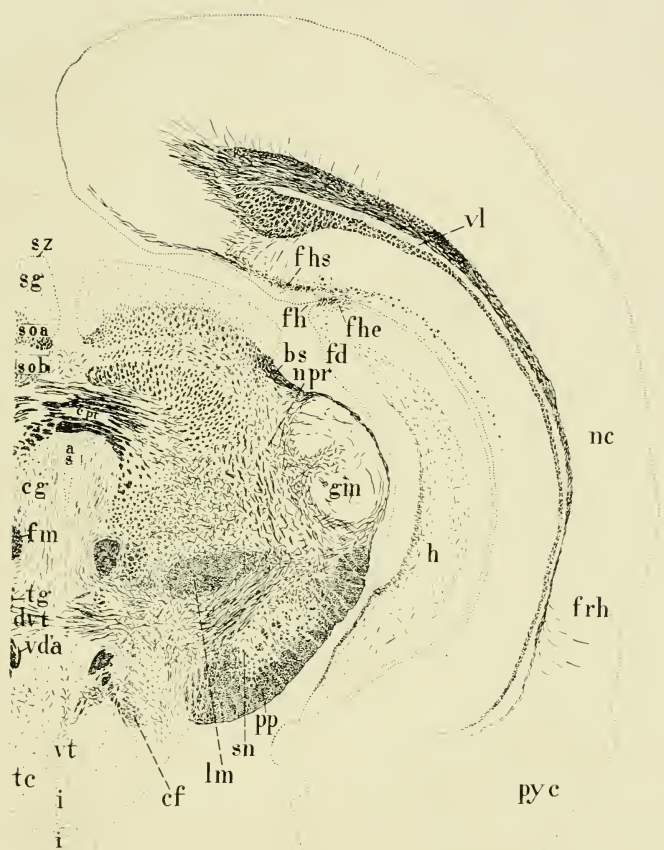
Plate XVII.   as, aqueduct of Sylvius; cf, column of fornix; cha, habenu-
     lar commissure; cpt, posterior commissure; cs, subthalamic nucleus;
     fd, fascia dentata; fe, endorhinal groove; fh, hippocampal fissure;
     fhe, external hippocampal fibres; fhs, fasciculus hippocampo-sub-
     splenialis; fm, fasciculus retroflexus; frh, rhinal fissure; gl, lateral
     geniculate body; gm, medial geniculate body; h, hippocampus; i,
     infundibulum; lm, medial lemniscus; nc, neocortex; npr, posterior
     nucleus of thalamus; pp, basis pedunculi; pyc, pyriform cortex;
     tc, tuber cinereum; toh, olfacto-hypothalamic tract; tro, optic
     tract; vd'a, mamillo-thalamic tract; vl, lateral ventricle; vt, third
     ventricle; zi, zona incerta.
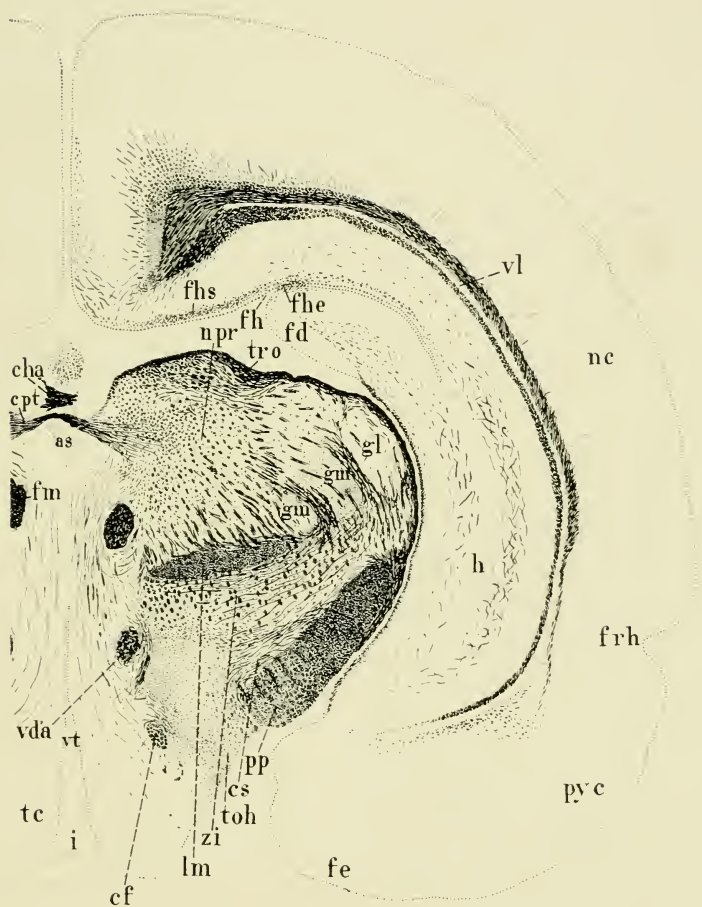
PLATE XVII

Plate XVIII. a, alveus; ab, basal nucleus of amygdala; al, lateral nucleus of amygdala; am, medial nucleus of amygdala; cc, corpus callosum; ce, external capsule; cf, column of fornix; chd, dorsal hippocampal commissure; cm, commissure of Meynert; cn, cingulum; co, cortical nucleus of amygdala; cs, subthalamic nucleus; fd, fascia dentata; fe, endorhinal groove; fhe, external hippocampal fibres; fhs, fasciculus hippocampo-subsplenialis; fim, fimbria; fm, fasciculus retroflexus; frh, rhinal fissure; gld, dorsal nucleus of lateral geniculate body; glv, ventral nucleus of lateral geniculate body; h, hippocampus; hl, lateral nucleus of habenula; hm, medial nucleus of habenula; i, infundibulum; in, indusium griseum; l, lateral nucleus of thalamus; lm, medial lemniscus; m, medial nucleus of thalamus; mi, inter-mediate mass; nc, neocortex; npa, parependymal nucleus; pp, basis pedunculi; pyc, pyriform cortex; sm, stria medullaris thalami; st, stria terminalis; tc, tuber cinereum; toh, olfacto-hypothalamic tract; v, ventral nucleus of thalamus; vd'a, mamillo-thalamic tract; vl, lateral ventricle; zi, zona incerta.

PLATE XVIII

Plate XIX.   a, alveus; ab, basal nucleus of amygdala; ac, central nucleus of amygdala; al, lateral nucleus of amygdala; am, medial nucleus of amygdala; cc, corpus callosum; ce, external capsule; cf, column of fornix; chd, dorsal hippocampal commissure; cho, optic chiasma; cin, internal capsule; cn, cingulum; co, cortical nucleus of amygdala; cp, caudate nucleus+putamen; fd, fascia dentata; fe, endorhinal groove; fhe, external hippocampal fibres; fhs, fasciculus hippocampo-subsplenialis; fim, fimbria; fos, fornix superior; frh, rhinal fissure; gp, globus pallidus; h, hippocampus; hl, lateral nucleus of habenula, hm, medial nucleus of habenula; in, indusium griseum; l, lateral nucleus of thalamus; lb, longitudinal amygdalo-pyriform association bundle (*sagittales Längsbündel*);   m, medial nucleus of thalamus; mi, intermediate mass; nbo, praeoptic nucleus; nc, neocortex; nl, nucleus reticularis thalami (lattice nucleus); npa, parependymal nucleus; nre, nucleus reuniens; pp, basis pedunculi; pyc, pyriform cortex; sm, stria medullaris thalami; st, stria terminalis; stI, commissural bundle of stria terminalis; toh, olfacto-hypothalamic tract; v, ventral nucleus of thalamus; vd'a, mamillo-thalamic tract;   vl, lateral ventricle; vt, third ventricle; 2, 3, fibres of stria terminalis connecting with amygdala; zi, zona incerta.

Plate XIX
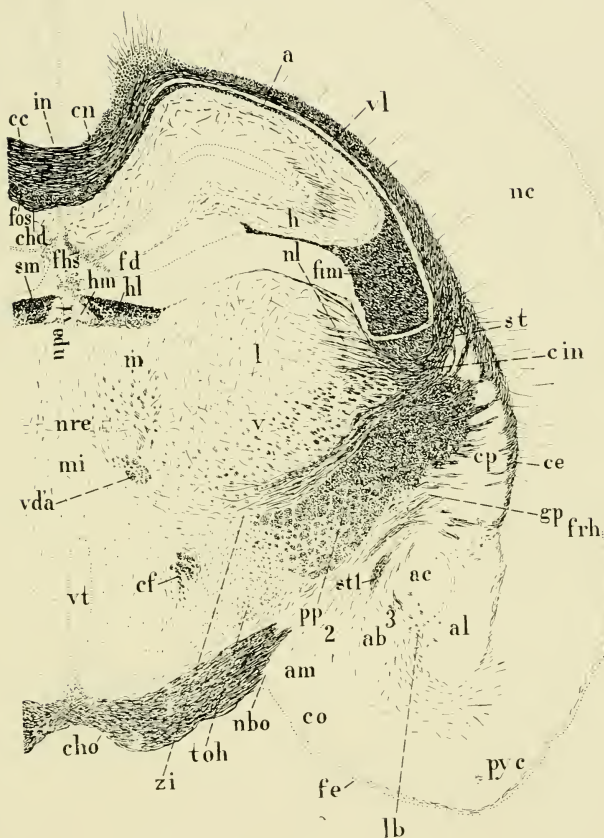
Plate XX. a, alveus; ac, central nucleus of amygdala; ad, dorso-medial part of anterior nucleus of thalamus; al, lateral nucleus of amygdala; av, ventro-lateral part of anterior nucleus of thalamus; ca, fibres from anterior commissure; cc, corpus callosum; ce, external capsule; cf, column of fornix; chd, dorsal hippocampal commissure; cho, optic chiasma; cin, internal capsule; cla, claustrum; cn, cingulum; cra, corona radiata; fd, fascia dentata; fe, endorhinal groove; fim, fimbria; fos, fornix superior; frh, rhinal fissure; gp, globus pallidus; h, hippocampus; hm, medial nucleus of habenula; in, indusium griseum; lb, longitudinal amygdalo-pyriform association bundle; m, medial nucleus of thalamus; mi, intermediate mass; nbo, praeoptic nucleus; nl, nucleus reticularis thalami; npa, parependymal nucleus; nre, nucleus reuniens; ntol, nucleus of lateral olfactory tract; pu, putamen; pyc, pyriform cortex; sm, stria medullaris thalami; sma, part of antero-ventral continuation of stria medullaris thalami; st, stria terminalis; stI, commissural bundle of stria terminalis about to end in ntol; toh, olfacto-hypothalamic tract in medial forebrain bundle, here mingled with diagonal band of Broca; tol, lateral olfactory tract; v, ventral nucleus of thalamus; vd'a, mamillo-thalamic tract; vl, lateral ventricle; 2, terminal fibres from stria terminalis.

PLATE XX
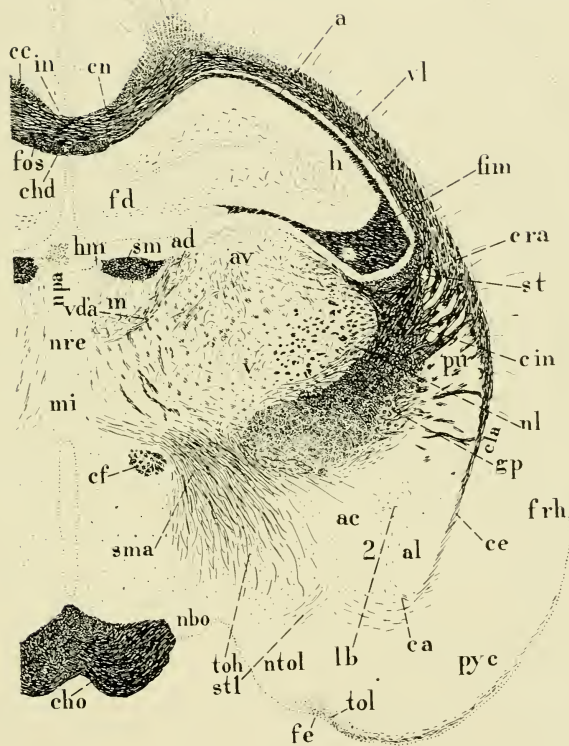
Plate XXI.   caa, anterior division of anterior commissure; cat, temporal division of anterior commissure; cau, caudate nucleus; cb, bed of anterior commissure; cc, corpus callosum; ce, external capsule; cf, column of fornix; chv, ventral or principal hippocampal commissure; cin, internal capsule; cla, claustrum; cn, cingulum; cra, corona radiata; db, diagonal band of Broca; fbl, lateral division of medial forebrain bundle (olfacto-hypothalamic fibres, stria medullaris, etc.); fbm, medial division of medial forebrain bundle (olfacto-hypothalamic tract, etc.); fe, endorhinal groove; fim, fimbria; fos, fornix superior; frh, rhinal fissure; gp, globus pallidus; in, indusium griseum; nc, neocortex; op, optic nerve; pu, putamen; pyc, pyriform cortex (lateral olfactory gyrus); sb, bed of stria terminalis; st, stria terminalis; to, tuberculum olfactorium; tol, lateral olfactory tract; vl, lateral ventricle.
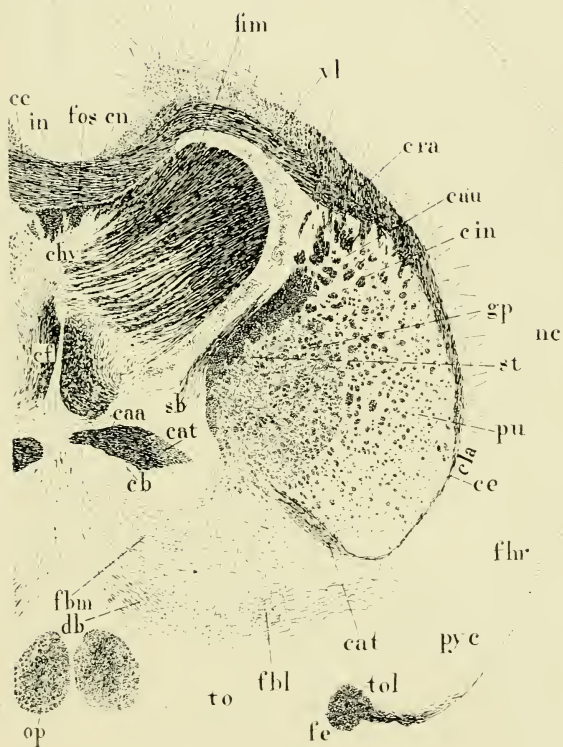
PLATE XXI

Plate XXII. caa, anterior limb of anterior commissure; cau, head of caudate nucleus; cc, corpus callosum; ce, external capsule; cf, column of fornix; cin, internal capsule; cla, claustrum; cn, cingulum; db, diagonal band of Broca mingled with other fibres of praecommissural system; fbl, lateral division of medial forebrain bundle; fe, endorhinal groove; fos, fornix superior; frh, rhinal fissure; in, indusium griseum; nac, nucleus accumbens septi; nc, neocortex; pc, praecommissural system of fibres running through nucleus of diagonal band of Broca; pyc, pyriform cortex (lateral olfactory gyrus); s, septum (the letter is in the pallial part of Johnston—his *primordium hippocampi*); to, tuberculum olfactorium; tol, lateral olfactory tract; vl, lateral ventricle.
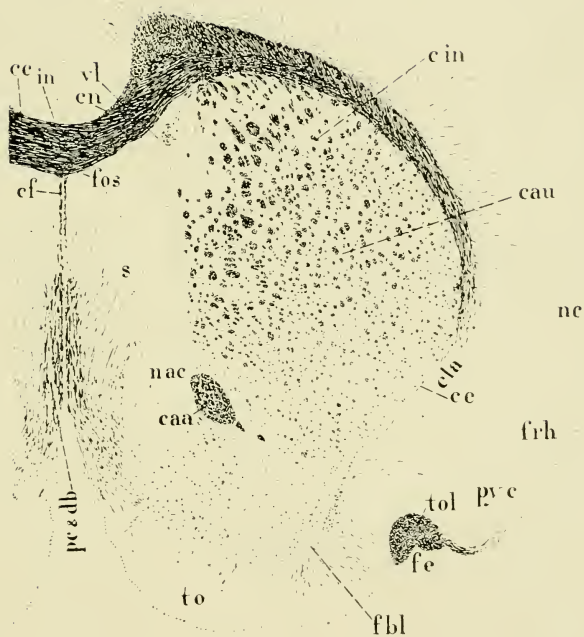
PLATE XXII

Plate XXIII.   caa, anterior limb of anterior commissure; cau, head of caudate nucleus; cin, internal capsule; cn, cingulum; fe, endorhinal groove; frh, rhinal fissure; h, rostral extension of hippocampal cortex; nc, neocortex; pyc, pyriform cortex (lateral olfactory gyrus); to, tuberculum olfactorium; toc, olfacto-cortical tract; tol, lateral olfactory tract; tom, medial olfactory tract; vl, lateral ventricle.

Plate XXIII
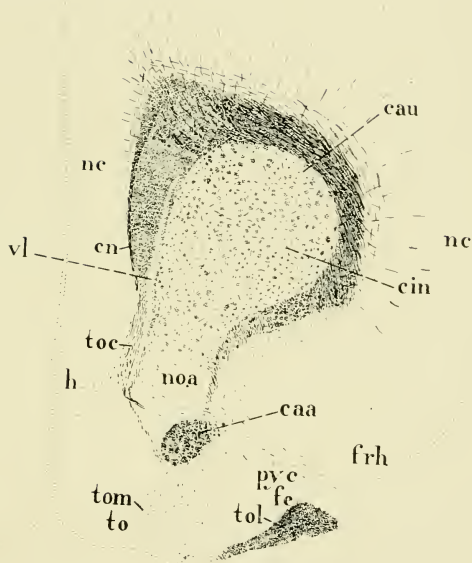
Plate XXIV.   frh, rhinal fissure; irh, incisura rhinica;   mp, white matter of the lateral olfactory gyrus containing the fibres of the anterior limb of the anterior commissure; nc, neocortex; soi, fibres of inter- mediate olfactory stria;   tol, lateral olfactory tract;   tom, medial olfactory tract; vl, rhinocoele (anterior extension of lateral ventricle); w, central white matter of cerebral hemisphere.

PLATE XXIV
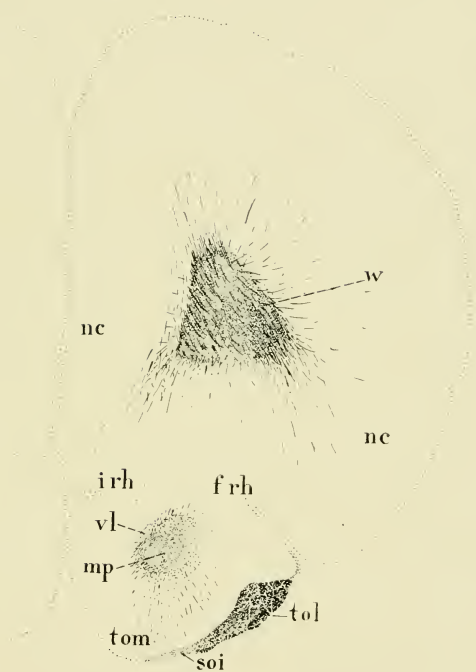
Plate XXV. bp, parolfactory bulb; lce, layer of mitral cells; lf, layer of olfactory nerve fibres; lge, external granular layer; lgel, gelatinous layer; lgi, internal granular layer; lgl, glomerular layer; lmp, layer of fibres of the white matter of the lateral olfactory gyrus including anterior commissure fibres; lto, layer of fibres of the olfactory tract; nc, neocortex on frontal pole of cerebral hemisphere; vrh, rhinocoele.

PLATE XXV

ne

bp

lf

lto

lmp

vrh

lgi

lgl

lf

lge

lgel

lce
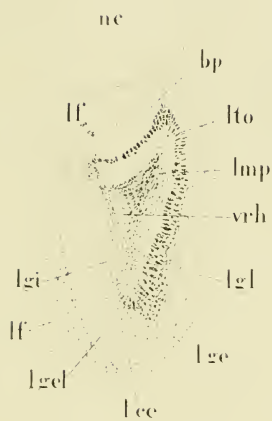
Plate XXVI. Parasagittal section of the brain of an adult albino rat, passing fully half a millimeter to one side of the median plane anteriorly and a little farther from it posteriorly. ×9.4.

ca, anterior commissure; cc, corpus callosum; cf, column of fornix; cg, central gray matter round aqueduct of Sylvius; chd, dorsal hippocampal commissure; cho, optic chiasma; chs, thin part of dorsal hippocampal commissure (section lies a little too far laterad to cut fornix superior); chv, ventral hippocampal commissure; ci, posterior colliculus; cma, mamillary body; cpt, posterior commissure; csu, anterior colliculus; ct, trapezoid body; dbc, decussation of brachia conjunctiva; dp, lateral fibres of pyramidal decussation; fd, fascia dentata; fhs, fasciculus hippocampo-subsplenialis; fm, fasciculus retroflexus; fs, fasciculus solitarius; ge, genu of corpus callosum; gVII., genu of motor root of facial nerve; h, hippocampus; hl, lateral nucleus of habenula; lm, medial lemniscus; nc, neocortex of cerebral hemisphere; nfs, nucleus of fasciculus solitarius; ng, nucleus gracilis; ni, interpeduncular nucleus; nrm, magno-cellular portion of red nucleus; nt, nucleus of trapezoid body; oi, inferior olivary nucleus; p, pyramidal tract; pc, praecommissural fibre system; pm, peduncle of mamillary body; po, pons; ro, rostrum of corpus callosum; s, septum; sm, stria medullaris thalami; sp, splenium of corpus callosum; tc, tuber cinereum; tg, mamillo-tegmental tract; th, thalamus; to, tuberculum olfactorium; tro, optic tract; vd'a, mamillo-thalamic tract; ve, fourth ventricle; vma, anterior medullary velum; vmp, posterior medullary velum; III., oculomotor nerve root; IV., decussating trochlear nerve roots; VI., abducent nerve root; VII., motor root fibres of facial nerve; VIII.c, chief vestibular nucleus; XII., hypoglossal nerve root.

PLATE XXVI

Plate XXVII. On the left, a diagram of the cell-lamination in a small part of the occipital cortex of an adult albino rat. On the right, a drawing of the blood vessels in the same piece of cortex. × 112. I., lamina zonalis; III., lamina pyramidalis; IV., lamina granularis interna; V., lamina ganglionaris; VI., lamina multiformis.

PLATE XXVII
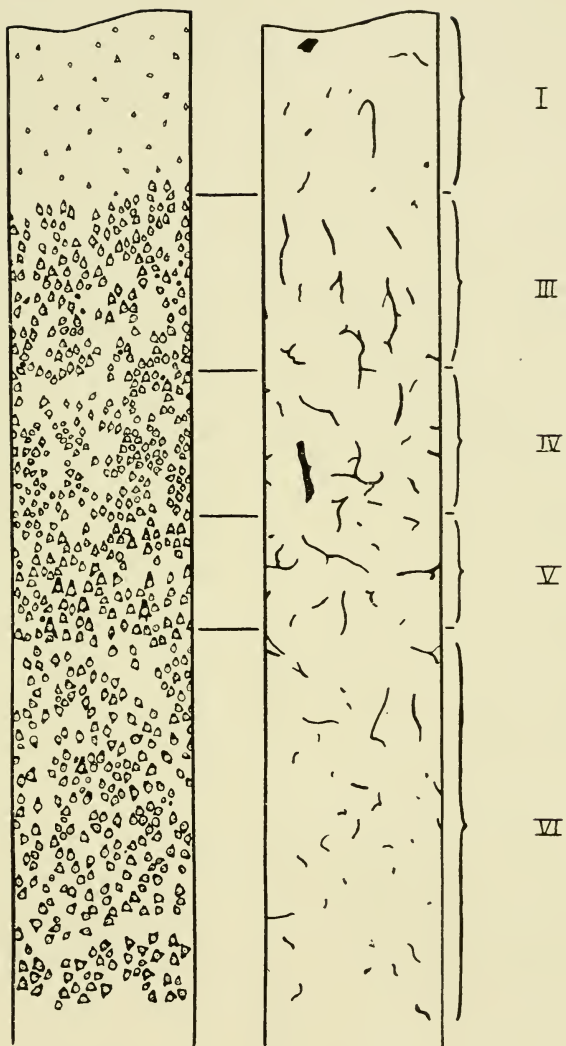
Plate XXVIII.   Diagrams of the dorsal and ventral surfaces of the brain of the albino rat, showing the approximate levels of the transverse sections represented in Plates VI.-XXV.   The numbers on the diagrams are those of the plates in which the corresponding sections are illustrated.

Plate XXVIII
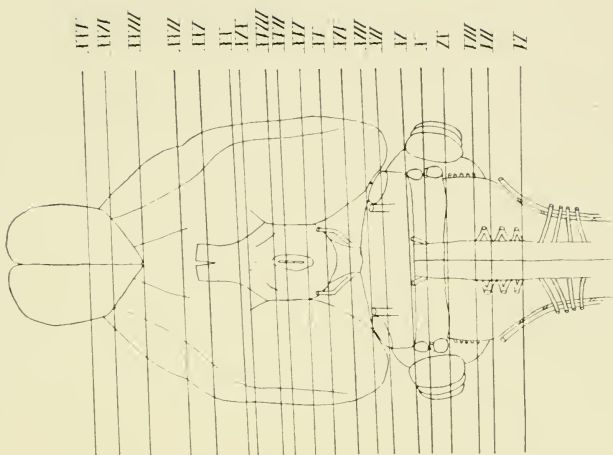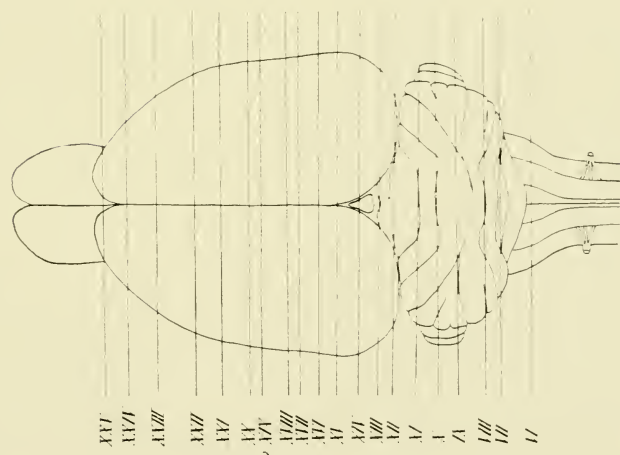
INDEX

Arabic numerals refer to pages, Roman numerals to plates.

185