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THE BRAIN

Sir James Crichton Browne
with the author's kind regards

THE

FUNCTIONS OF THE BRAIN

BY

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With numerous Illustrations

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1886

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PREFACE

TO

THE SECOND EDITION.

While my primary object in this edition has been, as before, to give a detailed account of my own investigations, I have endeavoured to present to the reader a systematic exposition of the functions of the brain and central nervous system in accordance with what seem to me, after extensive and critical survey, the best established facts of recent physiological and pathological research.

The book has been almost entirely re-written; a good deal has been added; and not a few modifications have been made, chiefly in matters of detail and methods of explanation. The principal doctrines formerly advocated in respect to the localisation of cerebral functions are maintained in all essentials unchanged.

In the preparation of this edition my grateful acknowledgments are due to Dr. Bevan Lewis, of the West Riding Asylum, for many beautiful sections and drawings illustrative of the structure of the brain and spinal cord; and to my colleague Dr. C. E. Beevor for much valuable assistance in general.

34 Cavendish Square: *October* 1886.

PREFACE

TO

THE FIRST EDITION.

My chief object in this book has been to present to the student of physiology and psychology a systematic exposition of the bearing of my own experiments on the functions of the brain. To do this satisfactorily I have thought it necessary to consider the functions of the cerebro-spinal system in general, with the view more especially of pointing out the mutual relations between the higher and the lower nerve centres. Throughout I have aimed at a concise digest rather than an encyclopædic account of the various researches by which our knowledge of the brain and spinal cord has been built up.

16 Upper Berkeley Street, Portman Square, W.:
October 1876.

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INTRODUCTORY.

THERE is, perhaps, no subject in physiology of greater importance and general interest than the functions of the brain, and there are few which present to experimental investigation conditions of greater intricacy and complexity. No one who has attentively studied the results of the labours of the numerous investigators in this field of research can help being struck by the want of harmony, and even positive contradictions, among the conclusions which apparently the same experiments and the same facts have led to in different hands. And when the seemingly well-established facts of experimentation on the brains of the lower animals are compared with those of clinical observation and morbid anatomy in man, the discord between them is frequently so great as to lead many to the opinion that physiological investigation on the lower animals is little calculated to throw true ight on the functions of the human brain. These discrepancies appear less unaccountable when the methods of experimentation and the subjects of experiment are taken into consideration. Up to quite a recent date, the principal method pursued by investigators into the functions of the brain consisted in observing the results following the destruction, by various means, of different parts of the encephalon.

The serious nature of the operations necessary to expose the brain for purposes of experiment, and the fact that the

various parts of the encephalon, though anatomically distinct, are yet so intimately combined and related to each other as to form a complex whole, make it natural to suppose that the establishment of lesions of greater or less extent in any one part should produce such general perturbation of the functions of the organ as a whole, as to render it at least highly difficult to trace any uncomplicated connection between the symptoms produced and the lesion as such. Moreover, the degree of evolution of the central nervous system, from the simplest reflex mechanism up to the highest encephalic centres, and the differences as regards the relative independence or subordination of the lower to the higher centres, according as we ascend or descend the animal scale, introduce other complications, and render the application of the results of experiment on the brain of a frog, or a pigeon, or a rabbit, without due qualification, to the physiology of the human brain, very questionable ; or even lead to conclusions seriously at variance with well-established facts of clinical and pathological observation. Notwithstanding these difficulties and discrepancies, many of which will be found, on careful examination, to be more apparent than real, experiments on animals, under conditions selected and varied at the will of the experimenter, are alone capable of furnishing precise data for sound inductions as to the functions of the brain and its various parts ; the experiments performed for us by nature, in the form of diseased conditions, being rarely limited, or free from such complications as render analysis and the discovery of cause and effect extremely difficult, and in many cases practically impossible. The discovery of new methods of investigation opens up new fields of inquiry, and leads to the discovery of new truths. The discovery of the electric excitability of the brain by Fritsch and Hitzig has given a fresh impetus to researches on the functions of the brain, and thrown a new light on many obscure points in cerebral physiology and pathology. Though great advances

have been made within the last ten years, much, however, still remains to be done. We are still only on the threshold of the inquiry, and it may be questioned whether the time has even yet arrived for an attempt to explain the mechanism of the brain and its functions. To thoughtful minds the time may seem as far off as ever; yet it is sometimes useful to review and systematise the knowledge we have so far acquired, if for no other reason than to show how much still remains to be conquered.

STRUCTURE

OF THE

BRAIN AND SPINAL CORD.

CHAPTER I.

STRUCTURE OF THE CEREBRO-SPINAL CENTRES.

§ 1. The following sketch of the anatomy of the cerebro-spinal system is intended mainly to facilitate the exposition of the details of the physiological and pathological investigations by which the functions of the brain and spinal cord have as yet been determined.

The minute anatomy of the brain and spinal cord is still in many respects exceedingly obscure. Some great facts have been firmly established by a concurrence of anatomical, physiological, and pathological research, but many others, founded merely on histological examination, partake more of the character of hypotheses than of demonstrated fact, and cannot be safely relied on either in support of or in opposition to the results of physiological or pathological experiments.

The difficulties of cerebro-spinal histology are enormous, and many connections and relations which are described by one set of investigators as real are found by others, equally competent, as merely apparent. Of the various ambitious and all too premature schemes of the minute structural relations of the cerebral and spinal tracts and centres proposed for our acceptance no two agree even in fundamental particulars.

Especially fruitful in reliable results of recent years, and likely to yield many more in years to come, has been the

Wallerian method of determining the structural and functional relations of the cerebro-spinal centres and tracts, by a study of the position and direction of the lines of degeneration induced by artificial or pathological lesions of certain parts of the brain and cord. In relation with this, also, facts of great value, but more open to varieties of interpretation, have been ascertained by embryological investigation of the respective periods and mode of development of the several cerebral and spinal tracts, which we owe mainly to Flechsig.[1] But as yet both methods have established comparatively little with any degree of certainty, and the great bulk of minute cerebro-spinal anatomy is in the most unsatisfactory state.

§ 2. The cerebro-spinal centres consist of the brain, or encephalon, contained within the skull, and the spinal cord, contained within the vertebral canal. The brain is in relation more or less direct with the periphery, by which is meant all the organs of receptivity and activity, by means of thirty-one pairs of spinal, and twelve (or, according to English anatomy, nine) pairs of cranial nerves. These nerves are separable into two great divisions, according to the nature of the functions which they subserve. The one set carry impressions from the periphery to the cord and brain, and are therefore called *afferent* nerves; while the other convey impulses from the brain and cord to the periphery, and are therefore termed *efferent*. The most prominent functions performed by these nerves being the conveyance of sensory impressions and motor stimuli respectively, the restricted terms *sensory* and *motor* are commonly employed in lieu of the wider terms afferent and efferent.

The spinal nerves are connected with the cord by two roots; the one of which, the efferent or motor (5, fig. 2), arises from the anterior or ventral aspect; the other, the afferent or sensory (6, fig. 2), from the posterior or dorsal aspect of the cord. The two roots remain separate for a short distance, during which the posterior passes through a ganglion (6′, fig. 2) or collection of nerve cells, and then unite to form one trunk (7, fig. 2), which is therefore a mixed nerve, composed both of afferent and efferent fibres.

[1] *Die Leitungsbahnen im Gehirn und Rückenmark*, 1876.

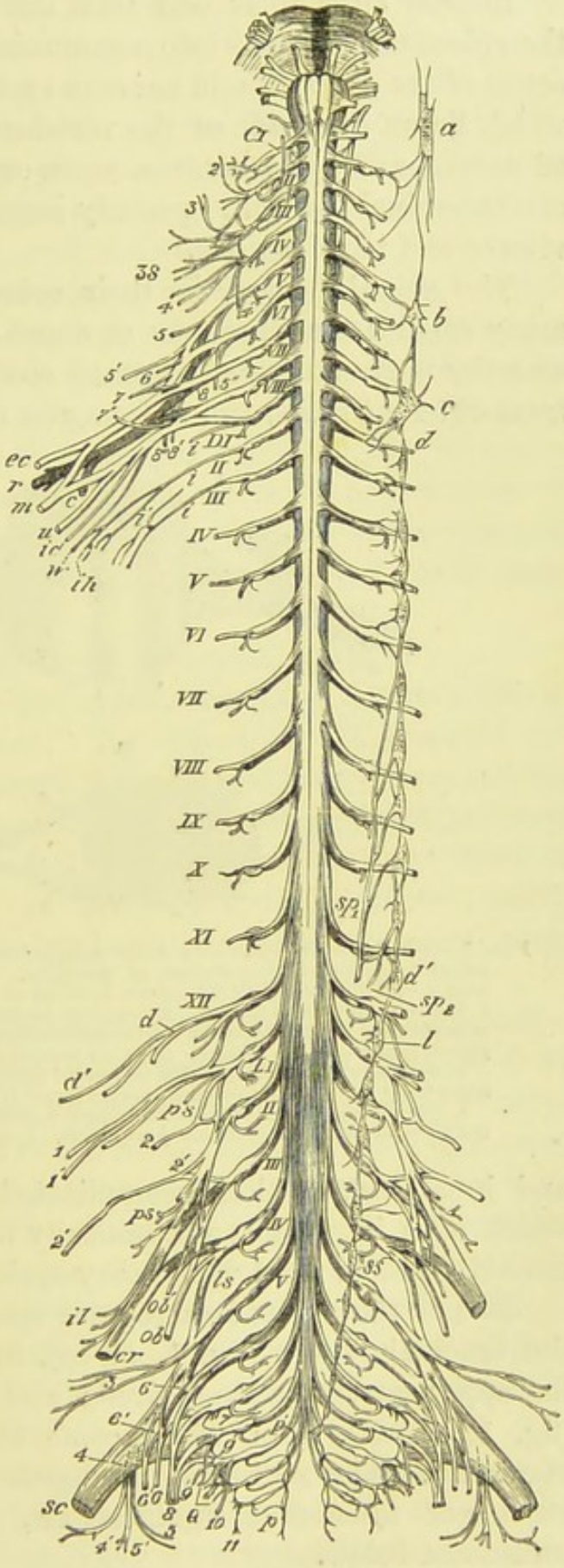


FIG. 1.—Diagram of the Cerebro-Spinal and Sympathetic Nerves.

This diagram, composed and modified after figures by Quain, represents the spinal cord as seen from before.

The spinal nerves are indicated by the Roman numerals :—CI–VIII being the cervical nerves; DI–XII, the dorsal; LI–V, the lumbar, and the rest, not specially numbered, the sacral nerves.

The plexiform arrangement of the nerves is seen on the left side.

The brachial plexus is seen to be composed of branches from CV to DI, with some communicating branches from CIV and DII; the lumbo-sacral plexus is seen to derive branches from LI to SIV inclusive.

The individual branches of these plexuses are indicated by letters and small numerals, but are not here named in detail.

The sympathetic cord and ganglia are seen on the right side, with their junctions with the spinal nerves. *a*, the superior cervical ganglion; *b*, the middle cervical ganglion; *cd*, the inferior cervical ganglion, united with the first dorsal ganglion; sp_1, the great splanchnic nerve; sp_2, the lesser splanchnic nerve; *d'*, the eleventh dorsal ganglion; *ss*, the upper sacral ganglion.

Shortly after their exit from the intervertebral foramina the spinal nerves enter into communication with the gangliated cords of the sympathetic nervous system (fig. 1, *a*, *b*, *c*, *d*, &c.) which lie on each side of the vertebral column. This system of nerves and nerve centres, more or less independent of the cerebro-spinal system, specially innervates the walls of the viscera and blood-vessels.

The spinal nerves, in their course to the periphery, in many cases form junctions or anastomoses with each other, whereby nerve trunks are formed composed of nerves derived from different roots, and these again form subsidiary divisions

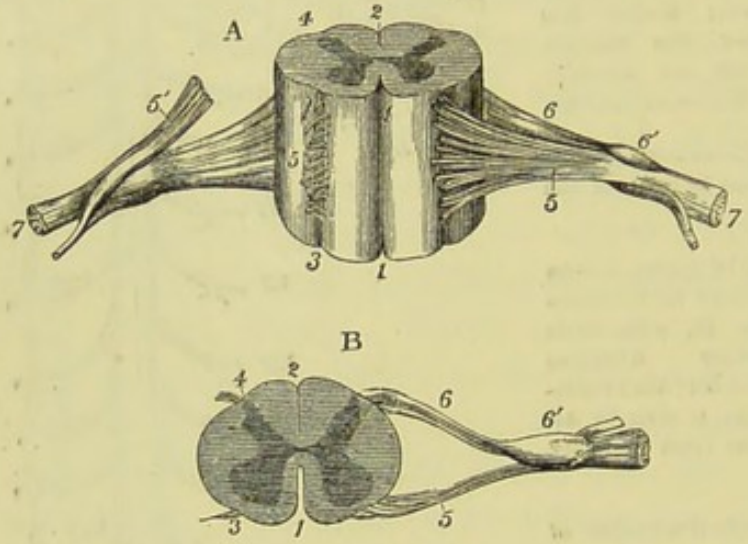


FIG. 2.—Spinal Cord (Quain).—In A the anterior surface of the cord is shown, the anterior nerve root being divided on the right. In B a transverse section of the cord is exhibited, showing the crescentic shape of the grey matter in the interior. 1, the anterior median fissure. 2, posterior median fissure. 3, anterior lateral depression over which the anterior nerve roots are seen to spread. 4, posterior lateral groove into which the posterior roots are seen to sink.

The anterior column is included between 1 and 3; the lateral column between 3 and 4; and the posterior column between 4 and 2.

5. The anterior root. 5′ in A=the anterior root divided. 6, the posterior roots, the fibres of which pass into the ganglion 6′. 7, the united or compound nerve.

and junctions; so that a complicated plexus is the result, in which it is impossible anatomically to trace the fibres of the individual roots from which they spring.

Two of these plexuses require special consideration; viz. the brachial plexus (fig. 1, CV–DI), from which the nerves of the upper extremity are derived; and the lumbo-sacral plexus (fig. 1, LI–SIV), from which come the nerves of the lower extremity. The plexiform arrangements of the nerves have important functional significations, some of which will be considered below.

§ 3. The spinal cord, which in man extends from the upper border of the atlas to the second lumbar vertebra, where it tapers to a point (*filum terminale*), is uniformly cylindrical in shape except at the points of origin of the roots forming the brachial and lumbo-sacral plexuses. Here the diameters are increased, giving rise to the cervical and lumbar enlargements respectively (fig. 1). The cord is divided into two symmetrical halves by the anterior and posterior longitudinal fissures (*a f*, *p f*, figs. 3, 4, 5), and the two halves are connected together by a commissure, which is seen on cross section to be formed by an anterior portion, situated at the bottom of the anterior fissure, and termed the *white commissure* (*a c*, fig. 3), and a grey portion, the *grey commissure* (*p c*), in which there is a more or less distinct canal, the *central canal* (*c c*), which is the remnant of the hollow tube from which both cord and brain were developed.

The cord is composed of grey and white matter.

The grey matter has the appearance of a double crescent united by the commissure. The horns of the crescent are termed the anterior (A) and posterior (P) horns respectively. The shape of the horns varies at different parts of the cord (figs. 3, 4, 5), but in general the anterior horns are clubbed, and do not reach the surface, while the posterior horns are prolonged to the groove into which the posterior roots enter.

The grey matter of the anterior horns contains large multipolar nerve cells arranged in groups (*a e*, *a i*, in figs. 3, 4, 5), embedded in a dense spongy network composed largely of nerve fibres and fine processes of the nerve cells. Of the numerous branches of the multipolar cells one is continued as the axis cylinder of one of the fibres of the anterior roots. The others —the protoplasmic processes—help to form the dense network, of which the grey matter is largely composed, which connects together different cell groups, and probably forms the medium of communication between the cells and the various tracts with which they are in relation.

The grey matter of the posterior horns contains also some multipolar cells of smaller size and more spindle shape than those of the anterior horns. They are also much less numerous,

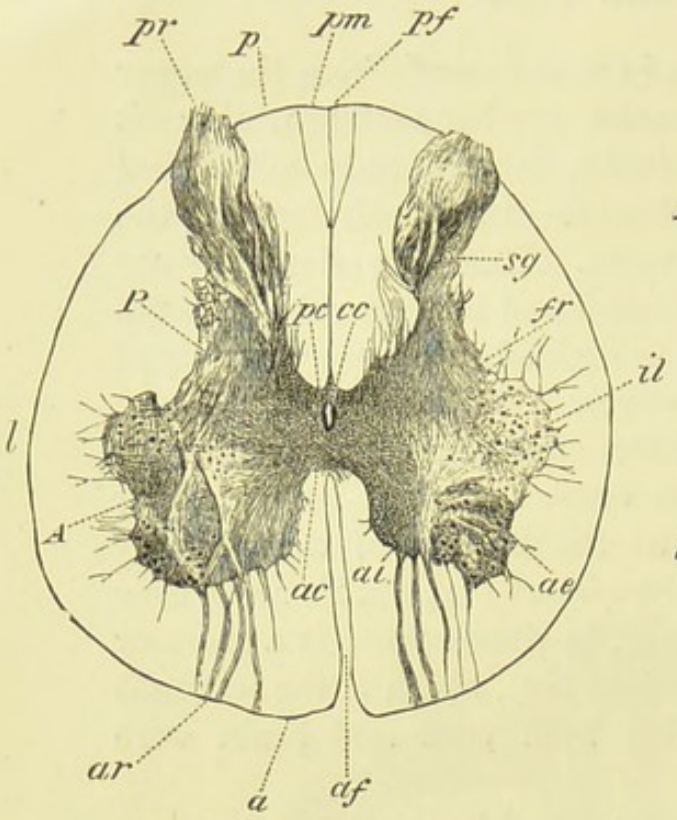


FIG. 3.—Transverse Section of Spinal Cord of Monkey. Lumbar region.
(From preparation and drawing by Bevan Lewis.)

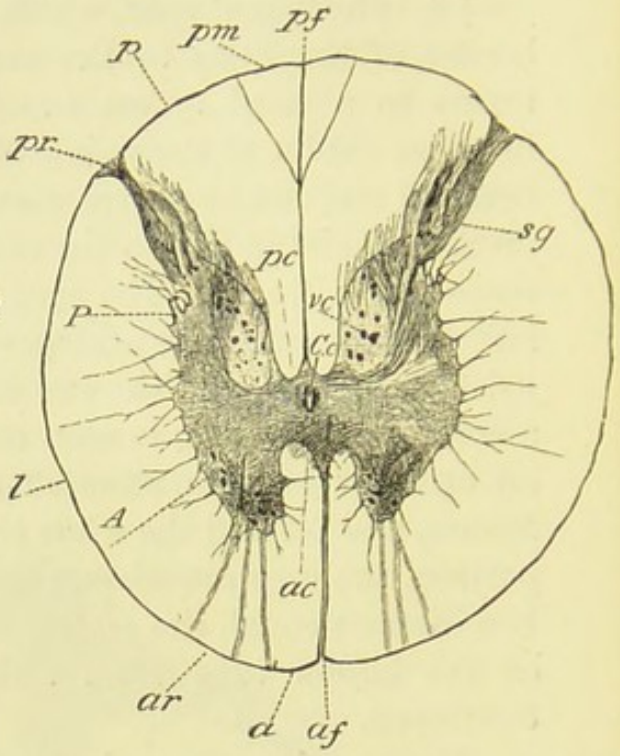


FIG. 4.—Transverse Section of Spinal Cord of Monkey. Dorsal region.
(From preparation and drawing by Bevan Lewis.)

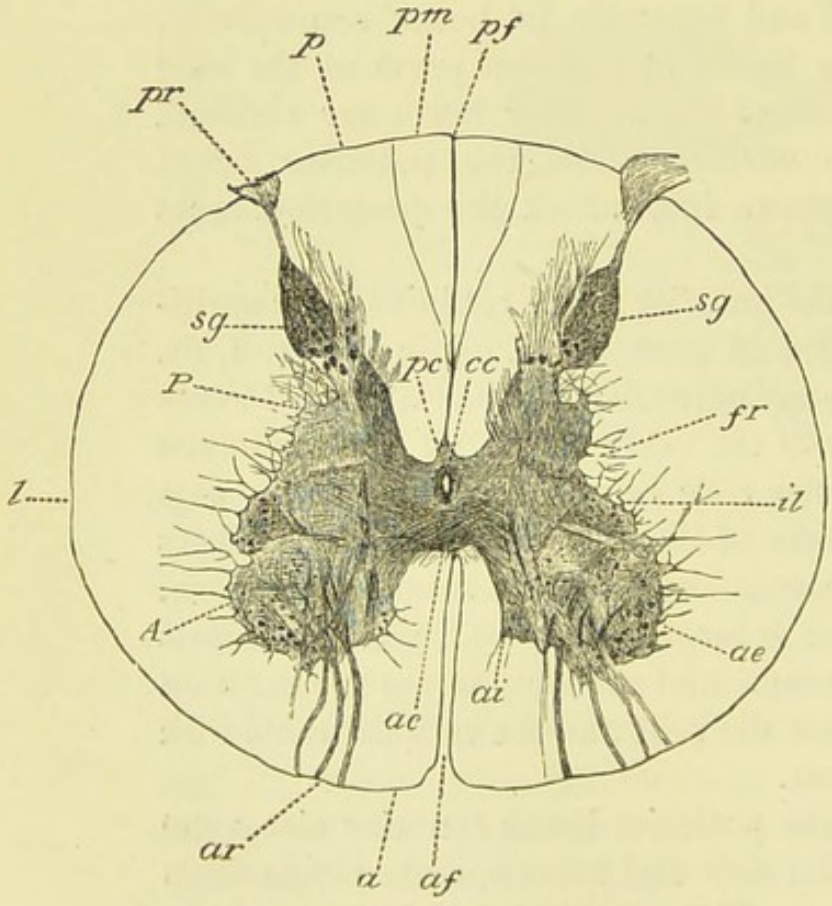


FIG. 5.—Transverse Section of Spinal Cord of Monkey. Cervical region.
(From preparation and drawing by Bevan Lewis.)

Description applicable to Figs. 3, 4, *and* 5.

A, anterior cornu. P, posterior cornu. *a*, anterior column. *l*, lateral column. *p*, posterior column. *ac*, anterior commissure. *ae*, external cell groups; and *ai*, internal cell groups of anterior cornu. *af*, anterior median fissure. *ar*, anterior roots. *cc*, central canal. *fr*, formatio reticularis. *il*, cells of tractus intermedio-lateralis. *vc*, Clarke's vesicular column. *pc*, posterior commissure. *pf*, posterior median fissure. *pm*, posterior median column (column of Goll). *pr*, posterior roots. *sg*, substantia gelatinosa.

and are not aggregated in groups. These cells also possess axis cylinder, and protoplasmic, processes. But whether the axis cylinder processes are directly connected with posterior nerve roots, as Deiters supposes, or pass in the direction of the anterior horns, as Gerlach holds, is not definitely determined, though certain facts in some of the lower vertebrates would support Deiters' view.

The apex of the posterior horns is covered by grey matter similar to that which surrounds the central canal, and is termed the *substantia gelatinosa* (*s g*, figs. 4, 5); but though this contains nerve elements it would seem, from the researches of Kühne, to consist mainly of a substance allied to keratin.

Besides the cells of the anterior and posterior horns proper other cell groups have received special designations. One of these, situated laterally to the anterior horn but more or less fused with it in the cervical and lumbar enlargements, is termed the postero-lateral, or *intermedio-lateral group* (*i l*, figs. 3, 5), and consists of cells of a spindle shape, and much smaller than those of the anterior horns generally. The other group, which is situated at the inner side of the base of the posterior horns, is termed *Clarke's vesicular column* (*v c*, fig. 4), and consists of multipolar cells, also considerably smaller than those of the anterior horns.

The grey matter viewed longitudinally forms a double column extending through the whole length of the cord. The width is not uniform. As has already been mentioned, there are special enlargements in the lumbar and cervical regions, and these are due mainly to the greater amount of grey matter in these situations. But throughout the whole cord the grey matter, more particularly of the anterior horns, is specially abundant at the junctions of the spinal nerves, so that a necklace arrangement is visible. This is seen much more distinctly in some of the lower vertebrates, and is an indication of the formation of the spinal cord of segments, more or less fused together, corresponding to the ventral ganglionic chain of the invertebrata (see fig. 41).

The cells of certain groups do not extend the whole length of the cord. Those of Clarke's vesicular column are found most distinctly in the region extending between the ninth

dorsal and third lumbar nerves. They are found continuously as high as the seventh cervical nerve. But homologous groups, more or less detached from the continuous column, are described as occurring as low as the origin of the second or third sacral nerve, and as high as the third cervical (Stilling). Ross[1] traces their homologues also in the cells forming the nucleus of the vagus, and Gaskell[2] arrives at the same conclusion.

§ 4. The white matter of the cord consists of tracts or columns of nerve fibres, which have received special names according to their position and connections.

The general term *anterior column* (*a*, figs. 3, 4, 5) is given to that tract which lies between the anterior median fissure and the point of emergence of the anterior roots. Between this point and the attachment of the posterior roots lies the *lateral column* (*l*, figs. 3, 4, 5), and between this and the posterior median fissure lies the *posterior column* (*p*).

But the Wallerian method, and the respective periods at which the nerve fibres of different tracts become invested with a medullary sheath, show that the columns are susceptible of further differentiation and specialisation.

The Pyramidal Tracts (fig. 6, P, P′).—These tracts, which are so called because they are continuous with the anterior pyramids of the medulla oblongata (fig. 7, *p a*), consist of two divisions, (1) the direct pyramidal tract, and (2) the lateral or crossed pyramidal tract. The direct tract, which is continuous with the pyramid of the same side, occupies the region of the anterior column immediately adjoining the anterior median fissure. It is also termed the *anterior median column* (fig. 6, T), or the *column of Türck*. The lateral pyramidal tract (fig. 6, P), which is continuous with the opposite pyramid, occupies the posterior portion of the lateral column external to the posterior cornu.

The pyramidal tracts diminish in size from above downwards, the direct tract ceasing about the middle of the dorsal region, while the lateral tract extends to the lower extremity

[1] *Diseases of the Nervous System*, 1881.

[2] 'The Structure, Distribution, and Function of the Nerves which innervate the Visceral and Vascular System,' *Journal of Physiology*, vol. vii. No. 1.

of the lumbar enlargement where it comes to the surface external to the apex of the posterior horn.

The pyramidal tracts are connected with the anterior horns of the spinal cord; the lateral or crossed tracts with the anterior horns on the same side on which they are situated, and the direct tracts with the same after crossing in the anterior commissure. Hence it would appear that the portions of the pyramid which do not decussate at the decussation of the pyramids of the medulla oblongata cross ultimately through the anterior commissure on their way downwards.

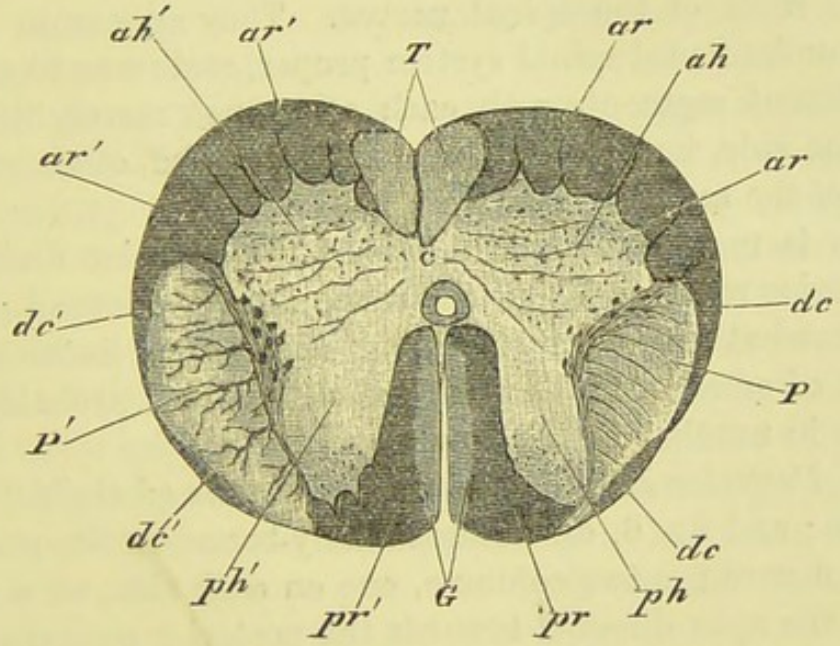


FIG. 6.—Transverse Section of Spinal Cord of Human Embryo at five months (Ross). *ah*, *ah'*, anterior horns of grey substance. *ph*, *ph'*, posterior horns. *ar*, *ar'*, anterior root zones. *pr*, *pr'*, posterior root zones. P, P', pyramidal fibres of lateral columns. T, columns of Türck. G, columns of Goll. *dc*, *dc'*, direct cerebellar tracts. *c*, anterior commissure.

The decussation is completed by the middle of the dorsal region, where the direct tracts cease generally to be visible.

The Direct Cerebellar Tracts (fig. 6, *d c*).—On the surface of the lateral pyramidal tract there is a flattened strand or column, first described by Foville, but more minutely investigated by Flechsig, which is traceable from the region of the second or third lumbar nerve up to the inferior peduncle of the cerebellum (fig. 9, *d c*). This tract receives fibres from the cells of Clarke's vesicular column (fig. 4, *v c*), and thus serves to connect these cells with the cerebellum.

The Anterior Root Zones (fig. 6, *a r*).—The antero-lateral columns which remain after elimination of the pyramidal and direct cerebellar tracts constitute the anterior root zones. In these an anterior portion and a lateral portion are differentiated, separated more or less by the lateral anterior roots, and also a portion which intervenes between the lateral pyramidal tract and the grey matter, termed by Flechsig the *lateral limiting zone* (fig. 3, *f r*).

The anterior root zones do not increase steadily from below upwards, like the tracts formerly described, but vary in size with the spinal segments, and the number and size of the anterior roots of the spinal nerves. They appear to belong to the fundamental spinal system proper, and serve to connect the different segments with each other, not merely those on the same side, but in part also those of the other side by means of the anterior commissure.

This is more particularly true of the anterior division of the anterior root zones, but the relations of the lateral portion are somewhat more complicated. The lateral limiting zone consists of smaller fibres than the others, and probably they increase in number from below upwards.

The Posterior Median Columns (*Columns of Goll*) (figs. 3, 4, 5, *p m*; and fig. 6, G).—Immediately bounding the posterior median fissure are two columns, one on each side, of a wedge shape—the apex directed towards the posterior commissure—which extend as distinct columns from the medulla oblongata to the middle of the dorsal region. Farther downwards they are not traceable as distinct columns in man, but in the monkey are distinct as far as the lumbar region (fig. 3, *p m*). These columns increase in size from below upwards.

The exact relations of these columns to the posterior roots and posterior horns are not in all respects agreed upon, but the experiments of Singer[1] would seem to demonstrate a direct continuity of some at least of the posterior roots in the column of Goll; for after section of the posterior roots of the upper sacral and lower lumbar nerves in a dog on the left side, he found a tract of degeneration in the posterior median

[1] *Sitzungsber. d. k. Acad. d. Wissensch.*, Bd. lxxxiv. Abth. iii. 1881.

column ascending all the way up to the medulla oblongata on the same side.

Posterior Root Zones (*Burdach's Columns*) (fig. 6, *p r*).—These are the portions of the posterior columns which remain after separation of the posterior median columns.

The dimensions of these columns vary with the number and size of the posterior roots of the spinal nerves. They appear to be formed mainly by the fibres of the posterior roots which enter them, but again leave them, after a longer or shorter course, to join the grey matter of the cord.

The Roots of the Spinal Nerves.—The most conflicting views still exist as to the course and connections of the anterior and posterior roots.

With respect to the *anterior roots* it appears well established that the majority, if not all (Laura), terminate primarily in the multipolar cells of one or other of the cell groups of the anterior horns through the axis-cylinder processes of these cells. From the cells of the anterior horn fibres pass into the lateral column of the same side, some also into the anterior column of the same side, and a considerable number through the anterior commissure to the anterior column of the opposite side. A passage of nerve roots to the median group of cells of the anterior horn of the opposite side has been described by Mayser, but this is not confirmed by the researches of Laura.[1]

Of the *posterior root* fibres some—the lateral division (see fig. 5)—enter the apex of the posterior horn, and penetrating the substantia gelatinosa diverge, brush fashion, horizontally in the direction of the anterior horns, as well as upwards and downwards into the substantia spongiosa. Others—the median division (see fig. 5)—enter the posterior columns and ascend in these a considerable distance before penetrating the grey matter. Some of the fibres, as would appear from the experiments of Singer above mentioned, ascend directly in the posterior median column, or column of Goll. Connections have been described between the posterior roots and the cells of Clarke's vesicular column, also with the solitary cells

[1] 'Sur la Structure de la Moelle Epinière,' *Archives Italiennes de Biologie*, tome i. fasc. ii. 1882.

of the posterior cornu, and with the lateral group of nerve cells of the anterior cornu.

From the cells of Clarke's column fibres pass into the direct cerebellar tract, as has been before mentioned.

The connections between the other cells, in which the posterior roots terminate, and the columns of the spinal cord, have been so differently described by Laura and others that nothing definite can be regarded as demonstrated. But it is probable, from physiological experiment, that the tracts of sensation decussate in the posterior commissure, and ascend in the opposite side of the cord, either in the posterior horns, or in the lateral tracts immediately adjacent to them.

§ 5. *The Medulla Oblongata.*—At the upper border of the atlas the spinal cord passes into the medulla oblongata, which extends from this point to the lower border of the *pons Varolii* (fig. 7, P V). The course and relations of the spinal centres and tracts here become exceedingly complex, owing to the intercalation of other centres, and multiple connections between the cerebellum and other encephalic centres.

The anterior longitudinal fissure of the spinal cord is continuous with a similar fissure on the anterior or ventral aspect of the medulla oblongata (fig. 7, *d*).

On each side of this are two pyramidal shaped columns, termed the *anterior pyramids* (fig. 7, *p a*), which decussate with each other more or less completely at the lower extremity of the fissure—the decussation of the pyramids. These tracts are continuous with the pyramidal tracts of the spinal cord. The greater portion of each pyramid is continuous with the lateral or crossed tract of the opposite side of the cord, while the smaller portion is continuous with the anterior median tract or column of Türck on the same side. But, as Flechsig has shown, the respective proportion of crossed and direct fibres in individual cases is liable to great variation; and in some rare cases there is no decussation at all, each pyramid passing directly into the anterior median column of the same side.

The rest of the anterior and lateral columns, or anterior root zones, are thrust out of their original position by the pyramids, and disappear beneath and around the *olivary*

body, which stands out with well-defined prominence on the antero-lateral aspect of the medulla oblongata (fig. 7, *o*).

The posterior median fissure of the spinal cord ceases abruptly at the lower posterior aspect of the medulla oblongata, by the opening up of the central canal of the spinal cord into the fourth ventricle, the sides of which constitute in a general

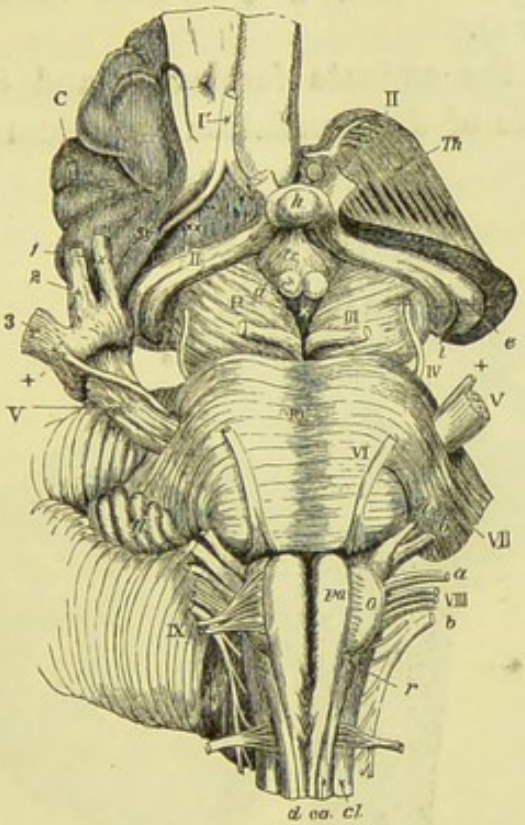


FIG. 7.—View from before of the Medulla Oblongata, Pons Varolii, Crura Cerebri, &c. (after Quain).—On the right side the convolutions of the central lobe, or Island of Reil, have been left; on the left the incision has been carried between the optic thalamus and the cerebral hemisphere. I', the olfactory tract cut short. II, the left optic nerve in front of the commissure. II', the right optic tract. *Th*. The cut surface of the left optic thalamus. *c*, the Island of Reil. *Sy*, the fissure of Sylvius. XX, locus perforatus anticus. *e*, the external, and *i* the internal corpus geniculatum. *h*, the hypophysis cerebri, or pituitary body. *tc*, tuber cinereum and infundibulum. *a*, one of the corpora albicantia. P, the peduncle, or crus cerebri. III, close to the left oculo-motor nerve. *x*, the locus perforatus posticus. *PV*, Pons Varolii. V, the greater root of the fifth nerve. +, the lesser or motor root; on the right side this is placed on the Gasserian ganglion. 1, 2, 3, the divisions of the fifth nerve. VI, the sixth nerve. VII *a*, the facial. VII *b*, the auditory. VIII, the pneumogastric. VIII *a*, the glosso-pharyngeal. VIII *b*, the spinal accessory. IX, the hypoglossal. *fl*, the flocculus. *pa*, the anterior pyramid. *o*, the olivary body. *r*, the restiform body. *d*, the anterior median fissure of the spinal cord, above which is the decussation of the pyramids. *ca*, the anterior column. *cl*, the lateral column of the spinal cord.

sense the restiform tracts or inferior peduncles of the cerebellum.

The point where the posterior median columns diverge is termed the *calamus scriptorius*. The columns which are the continuation of the columns of Goll are here called the

funiculi graciles, and they are seen to swell at the calamus into a club shape, owing to the development in each of a nucleus termed the *clavate nucleus* (fig. 8, 4).

Immediately external to the funiculi graciles are the columns which are continuous with the columns of Burdach, and are here called the *funiculi cuneati*. These also contain each a special nucleus of grey matter termed the *cuneate nucleus* (fig. 9, *n c*).

External to the cuneate fasciculus and nucleus another column is capable of differentiation; a column which is con-

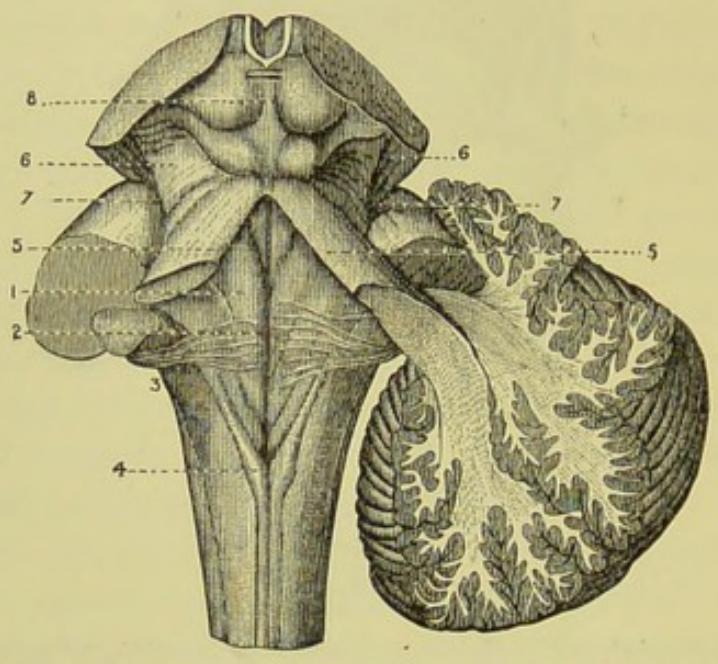


FIG. 8.—The Fourth Ventricle exposed by Division of the Cerebellum (Sappey).—On the left side the cerebellar peduncles have been cut short; on the right the middle peduncle has been cut short, while the superior and inferior retain their connections. 1, Median groove of the med. obl. bounded on each side by the *fasciculi teretes*. 2, striæ acusticæ. 3. inferior cerebellar peduncle or restiform body. 4, clavate nucleus. 5, superior cerebellar peduncle, or processus a cerebello ad cerebrum. 6, fillet. 7, crura cerebri. 8, corpora quadrigemina.

tinuous with the posterior horn of the spinal cord, but here considerably enlarged. The column is termed the column of Rolando, and the grey matter, the *tubercle of Rolando* (fig. 9, *t* R).

Into the restiform tract passes also a special division of the lateral column—the direct cerebellar tract (fig. 9, *d c*).

Other fibres are seen to proceed from the lateral aspect of the upper extremity of the restiform tract, and to cross the surface of the olivary body and pyramid to the middle line.

A special bundle of these arcuate fibres, which crosses beneath the lower margin of the olivary body, has received the name of the *arciform band* of Solly (fig. 9, *f a*).

Of these various columns and tracts the course of the anterior pyramids is alone clear. They ascend in the same relative position upwards through the pons to the crura cerebri (fig. 7, P).

When a transverse section is made of the medulla oblongata at the decussation of the pyramids (fig. 10) it is seen that, in consequence of the passage of the fibres from the lateral tracts to the pyramid of the opposite side, the anterior horns are detached from the central grey matter and pushed

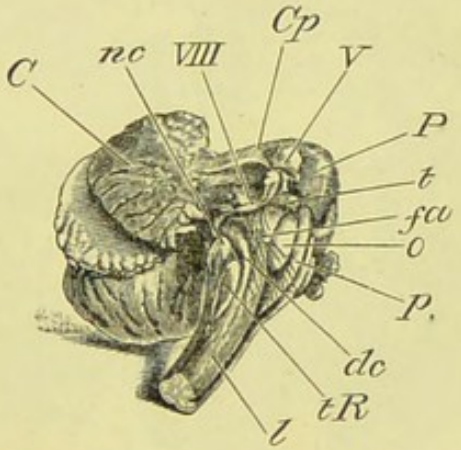


FIG. 9.—Dorso-lateral View of Medulla Oblongata of Monkey (nat. size).—C, cerebellum divided and partially dissected so as to show the middle peduncle. *cp*, middle peduncle. *dc*, direct cerebellar tract. *fa*, arciform fibres. *l*, lateral column. *nc*, nucleus cuneatus. *o*, olivary body. *p*, pyramid. *t* R, tubercle of Rolando. *t*, trapezium. V, fifth nerve. VIII, eighth or auditory nerve.

out laterally. The posterior horns also become much modified. While the basal portion adjacent to the central grey substance maintains its original position, the neck is prolonged out laterally, and the apex swells into a head, which is the beginning of the tubercle of Rolando (fig. 10, C *p*).

Posteriorly the grey matter of the funiculi graciles and funiculi cuneati begins to appear as offshoots from the basal portion of the posterior horns (fig. 10, N *g*, and N *c*). Higher up, where the central canal opens into the fourth ventricle, the basal portion of the grey matter forms a ring round the central canal, of which the ventral portion is the representative of the anterior horns, and the dorsal of the posterior. The detached portion of the anterior horns is represented only by collections

of cells laterally situated in an area which, owing to its aspect, is termed the reticular formation.

When a section is made at a level with the middle of the olivary bodies (fig. 11) the central canal is fully opened up, and the grey matter which formed the dorsal aspect of the central canal is spread out laterally on the floor of the fourth ventricle, while the ventral, or nuclei of the motor nerves, remains close to the middle line.

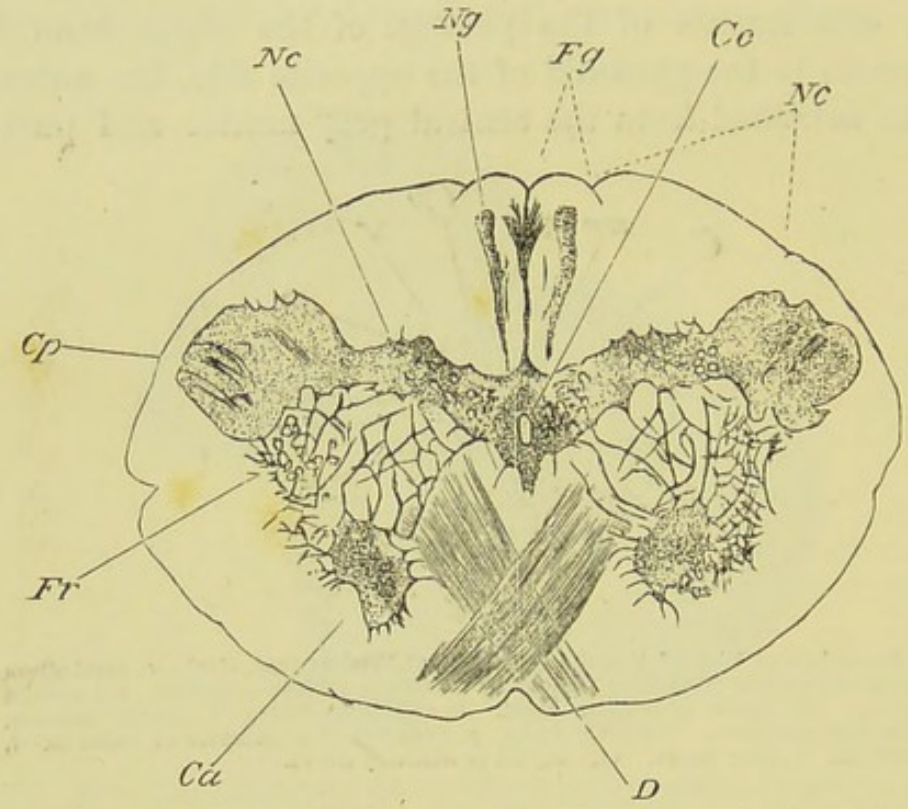


FIG. 10.—Section of the Medulla Oblongata of Monkey at the Decussation of the Pyramids. (From preparation and drawing by Bevan Lewis).—*Ca*, anterior cornu, with cell groups. *Cp*, posterior cornu, with fibres of the posterior roots of the first cervical nerve. Cc, central canal. D, decussation of pyramids. *Fg*, fasciculus gracilis. Fc, fasciculus cuneatus. *Ng*, clavate nucleus. Nc, cuneate nucleus. *Fr*, formatio reticularis.

The *olivary body* (fig. 11, o) has the appearance of a wavy capsule open towards the middle line, and contains a rich collection of small multipolar cells. Other aggregations of nerve cells more or less detached have received special names, (parolivary body, nucleus of the pyramid, fig. 11, A *ol*).

The pyramids pursue their course upwards in the same relative position as before. Between the pyramids, olivary bodies, and the grey matter and tracts on the posterior aspect of the medulla oblongata, the central area is occupied by the

reticular formation (fig. 11). This is divided by the roots of the hypoglossal or twelfth cranial nerve into a median area, A —bounded internally by the raphe, R—and a lateral area, L. The median area consists almost exclusively of medullary fibres, while the lateral area contains also numerous nerve cells. In both areas there is a complex interlacement of longitudinal and arciform fibres which cross the longitudinal bundles in all directions. Into the reticular formation are traceable the anterior root zones of the spinal cord, and in

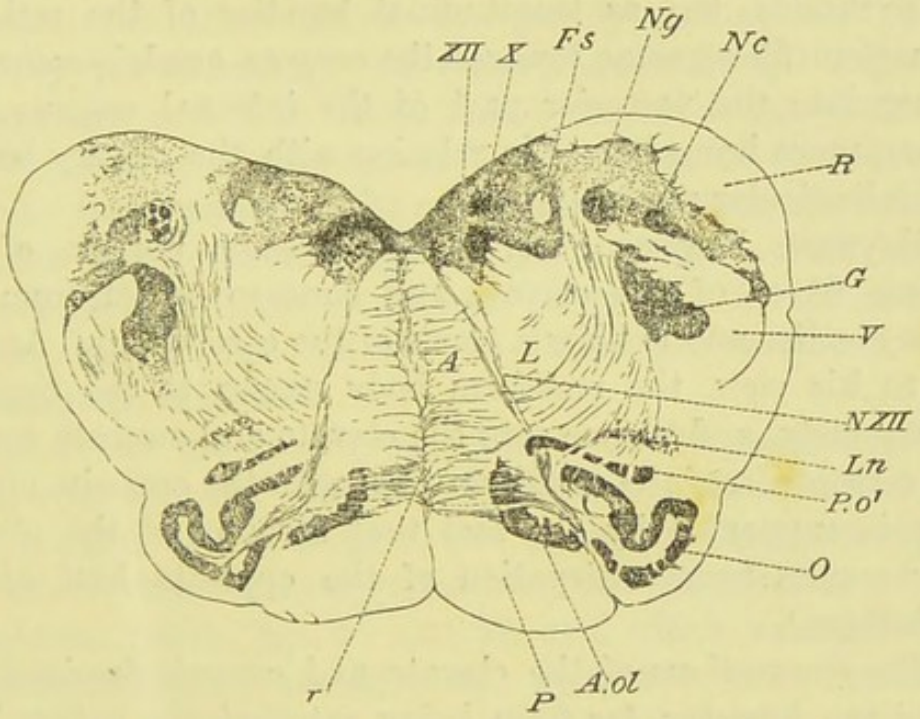


FIG. 11.—Medulla Oblongata of Monkey.—Section through the middle of the Olivary Bodies. (From a preparation and drawing by Bevan Lewis).—A, median portion of formatio reticularis. A *ol*, internal accessory olive. Fs, funiculus solitarius. G, tubercle of Rolando (substantia gelatinosa). L, lateral area of formatio reticularis. Ln, lateral nucleus. Nc, cuneate nucleus. Ng, clavate nucleus. O, olivary body. P, pyramid. R, restiform tract. *r*, raphe. V, ascending root of fifth nerve. X, nucleus of vagus. XII, nucleus of hypoglossal, and NXII, roots of hypoglossal nerve.

such manner that the zones of the anterior columns pass into the median area, and those of the lateral columns into the lateral area, where they come into relation with the scattered cells of the reticular formation and with the olivary body. These tracts are supposed to be connected above with the optic thalami and corpora quadrigemina.

Between the olivary bodies and just above and posterior to the decussation of the pyramids there is a well-marked decussation in the raphe of the medulla oblongata.

Meynert has described this as a decussation of the posterior

columns of the spinal cord. These apply themselves posterior and external to the pyramids, a position which, according to him, they retain in the foot of the crus cerebri (fig. 19).

Flechsig and others, however, deny that these fibres have any relation to the pyramids or outer fibres of the crus cerebri. Flechsig terms the region of decussation the *inter-olivary layer*. It is derived from fibres proceeding from the clavate and cuneate nuclei and olivary bodies. These decussate in this region and ascend upwards, not in relation with the pyramids, but as longitudinal bundles of the reticular formation (fillet), some towards the corpora quadrigemina and thence into the posterior part of the internal capsule, and others, more immediately in relation with the olivary bodies, to the lenticular nuclei (fig. 23).

Meynert, however, derives the greater portion of the arcuate fibres of the clavate and cuneate nuclei from the olivary bodies and restiform tracts of the cerebellum. According to his view, the restiform body passes to the opposite olivary body, and thence into the clavate and cuneate nuclei. The connection of the restiform tract with the opposite olivary body is supported by the fact that atrophy of the olivary body results from extirpation of the opposite half of the cerebellum.[1]

The connections of the clavate and cuneate fasciculi and nuclei are, however, far from being satisfactorily determined. Monakow[2] holds that some of the fibres of the cuneate fasciculus ascend to the cells of Deiters' nucleus (fig. 14, s), and some, perhaps, directly into the cerebellum.

The *restiform body* proper is the outer portion of the inferior cerebellar peduncle (fig. 11, R), also termed the restiform body in a general sense. Into this can be traced the direct cerebellar tract, which ascends, and, judging from the degeneration which ensues when it is cut, terminates in the upper vermiform process of the same side (Monakow). Besides this tract, and possibly some fibres from the cuneate nucleus, the restiform body is composed of arcuate fibres from the opposite olivary body, before mentioned, and also of fibres

[1] Gudden, *Neurologisches Centralblatt*, 1882.

[2] *Archiv f. Psychiatrie*, Bd. XIV. Heft 1.

(the external arciform fibres), which appear to be in relation with the pyramids, but which, as Edinger [1] supposes, may be really derived from the posterior columns through the inter-olivary layer.

§ 6. From the grey matter of the posterior aspect (tegmentum) of the medulla oblongata, and its upward continuation into the pons, spring the cranial nerves from the twelfth (ninth) to the fifth inclusive. Some of these—the twelfth (hypoglossal), the eleventh (accessory), the seventh (facial), the sixth (abducens oculi)—are purely motor; the eighth (auditory) purely sensory; the tenth (vagus), the ninth (glosso-pharyngeal), and fifth (trigeminal) mixed or sensori-motor nerves. The exact relations and connections of the nuclei of origin of these nerves would require a more elaborate description than can be included in the limits of this sketch, and it will suffice to indicate the general relations. In the accompanying figures (figs. 12 and 13) these are indicated in a diagrammatic manner.

Just before the opening up of the central canal into the fourth ventricle, the central grey substance which forms the basal portion of the anterior and posterior horns surrounds the canal. The ventral portion forms the nucleus of the hypoglossal nerve (figs. 11 and 12, XII), which emerges from the medulla between the olive and pyramid; while the dorsal position forms the nucleus of the accessory-vagus nerve (fig. 12, XI). A spinal nucleus of this nerve, which supplies the sterno-mastoid and trapezius muscles, is traceable to the lateral cells of the anterior horn of the spinal cord for some considerable distance below (fig. 12, XI).

With the opening of the central canal the ventral portion of the grey matter, or motor column, remains close to the middle line, while the dorsal portion is spread out laterally on the floor of the fourth ventricle, and forms a column which gives origin to the vagus and glosso-pharyngeal nerves (figs. 11, 12, X and XI).

On the lateral ventral aspect of the nucleus of the vagus a strand of fibres is seen—*funiculus solitarius*—(fig. 11, F *s*), which can be followed downwards in the cervical portion of

[1] *Neurolog. Centralblatt*, No. 4, 1885.

the cord. It is supposed to consist of fibres connecting the vago-accessorius and glosso-pharyngeal nuclei with the origin of the phrenic nerve, and hence called the *respiratory bundle* (Krause).

In the region of the striæ acusticæ a third collection of nerve cells appears, which are regarded as forming the nuclei of origin of the eighth or auditory nerve. The innermost of

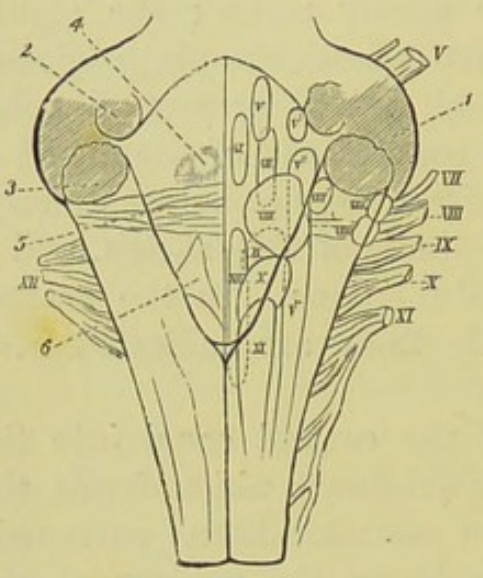


FIG. 12.—Diagram of the posterior aspect of the Medulla Oblongata, showing the position of the Nuclei of the Cranial Nerves. (After Erb.) V, motor nucleus. V′, middle, and V″, inferior sensory nucleus of the fifth nerve. VI, abducens nucleus. VII, facial nucleus. VIII, inner, and VIII′, outer auditory nucleus. VIII″ and VIII‴, divisions of the anterior auditory nucleus. IX, glosso-pharyngeal nucleus. X, vagus nucleus. XI, accessorius nucleus. XII, hypoglossal nucleus. 1, middle cerebellar peduncle. 2, superior cerebellar peduncle. 3, inferior cerebellar peduncle. 4, eminentia teres. 5, striæ acusticæ. 6, ala cinerea. V–XII, the respective cranial nerve roots.

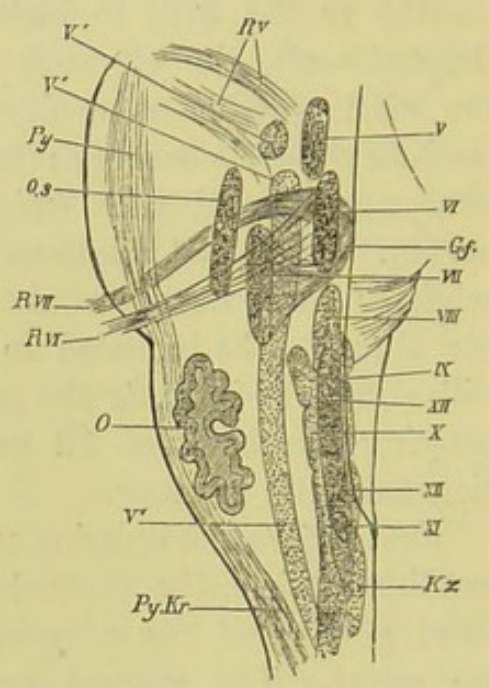


FIG. 13.—Diagrammatic representation of the Nuclei of the Cranial Nerves, as seen in section. The left half is supposed removed, and the nuclei nearer the median line are shaded darker than the others. (After Erb.) Py, pyramidal tracts. Py Kr, decussation of the pyramids. O, olivary body. Os, upper olivary body. V, motor, V′. middle sensory, and V″, lower sensory nucleus of the fifth nerve. VI, abducens nucleus. Gf, knee of the facial nerve. VII, facial nucleus. VIII, inner auditory nucleus. IX, glosso-pharyngeal nucleus. X, vagus nucleus. XI, accessorius nucleus. XII, hypoglossal nucleus. Kz, clavate nucleus. RV, roots of fifth nerve. RVI, roots of sixth or abducens. RVII, roots of facial.

this group is termed the posterior median or internal nucleus (figs. 12, 13, VIII; fig. 14, VIII^2).

External to this, and in close relation to the cerebellar peduncle, is another collection of cells, the lateral median or external nucleus, or *Deiters' nucleus* (fig. 14, s). Though it has been generally supposed that the auditory nerve is connected with this nucleus, this is disputed by Laura, and, as

before stated, Monakow considers that this nucleus is in relation with the cuneate fascicle. The later experiments of Vegas[1] do not, however, support Monakow's view. But that the cells of Deiters' nucleus are not related to the auditory nerve would appear to be proved by investigations of Onufrowicz,[2] which show that they undergo no atrophy after destruction of the auditory nerve or labyrinth. This author thinks that the relation of the posterior median nucleus (which Laura regards

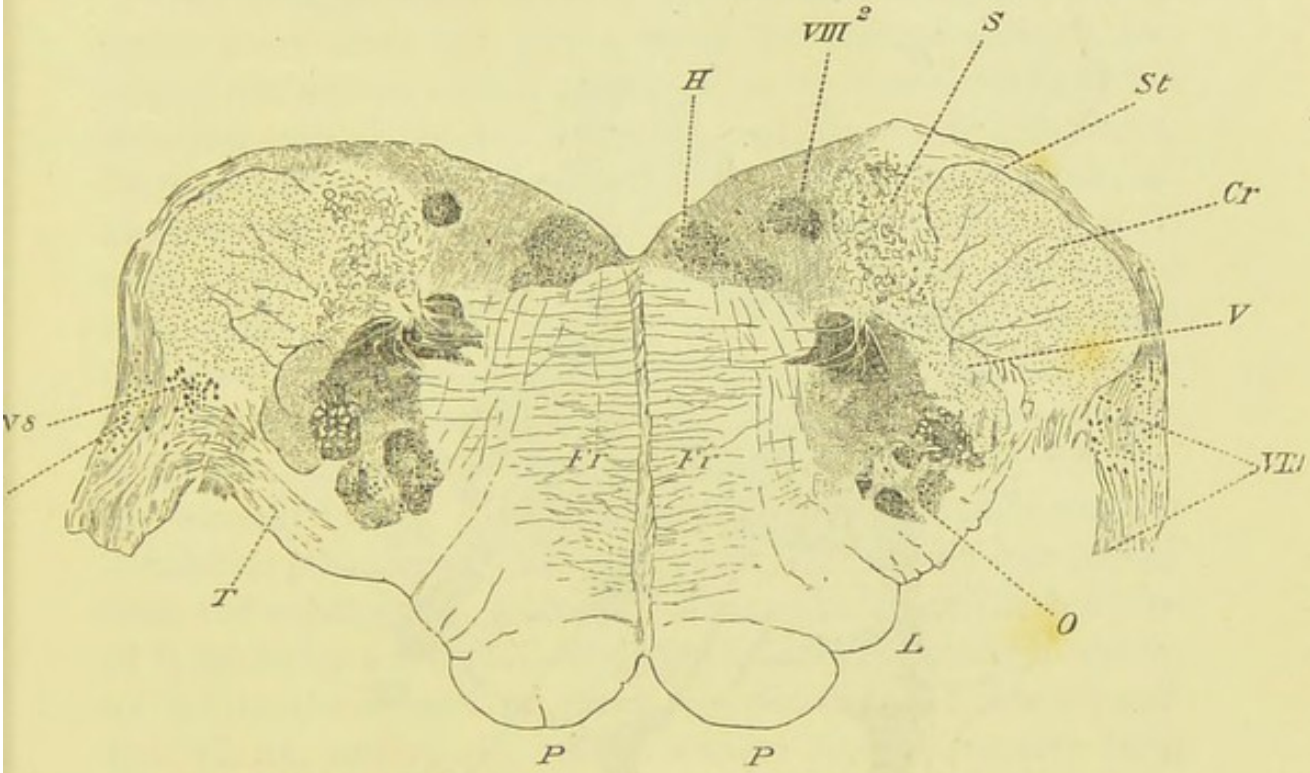


FIG. 14.—Medulla Oblongata of Monkey.—Section through the region of the striæ acusticæ. (From preparation and drawing by Bevan Lewis).—*Cr*, restiform body. *Fr*, formatio reticularis. H, upper extremity of hypoglossal nucleus. L, lateral column near the termination of the olivary body. N_a, anterior auditory nucleus. *Nr*, nerve cells of roots of auditory nerve. O, superior olivary body. P, pyramid. S, internal division of inferior cerebellar peduncle, Deiters' nucleus. *St*, striæ acusticæ. T, lowest fasciculi of trapezium. V, ascending root of fifth nerve. VIII, roots of auditory nerve. VIII², region of internal auditory nucleus.

as the principal nucleus) to the auditory nerve is doubtful, and his researches lead him to believe that the true origin of the auditory nerve is the semilunar shaped mass covering the origin of the inferior cerebellar peduncle, and corresponding with the tuberculum acusticum of some of the lower vertebrates (fig. 14, s *t*). The striæ acusticæ, which look like the direct continuations of the posterior roots of the auditory

[1] *Archiv f. Psychiatrie*, Bd. XVI. Heft 1.
[2] *Ibid.* Bd. XVI. Heft 3.

nerve, have no such direct relations. Perhaps they may be indirect paths or connections through the tuberculum acusticum, though, as they are sometimes wanting, even this is doubtful.

Another group of cells included in what is generally termed the anterior nucleus (fig. 12, VIII″, VIII‴; and fig. 14, N_8, N *r*),

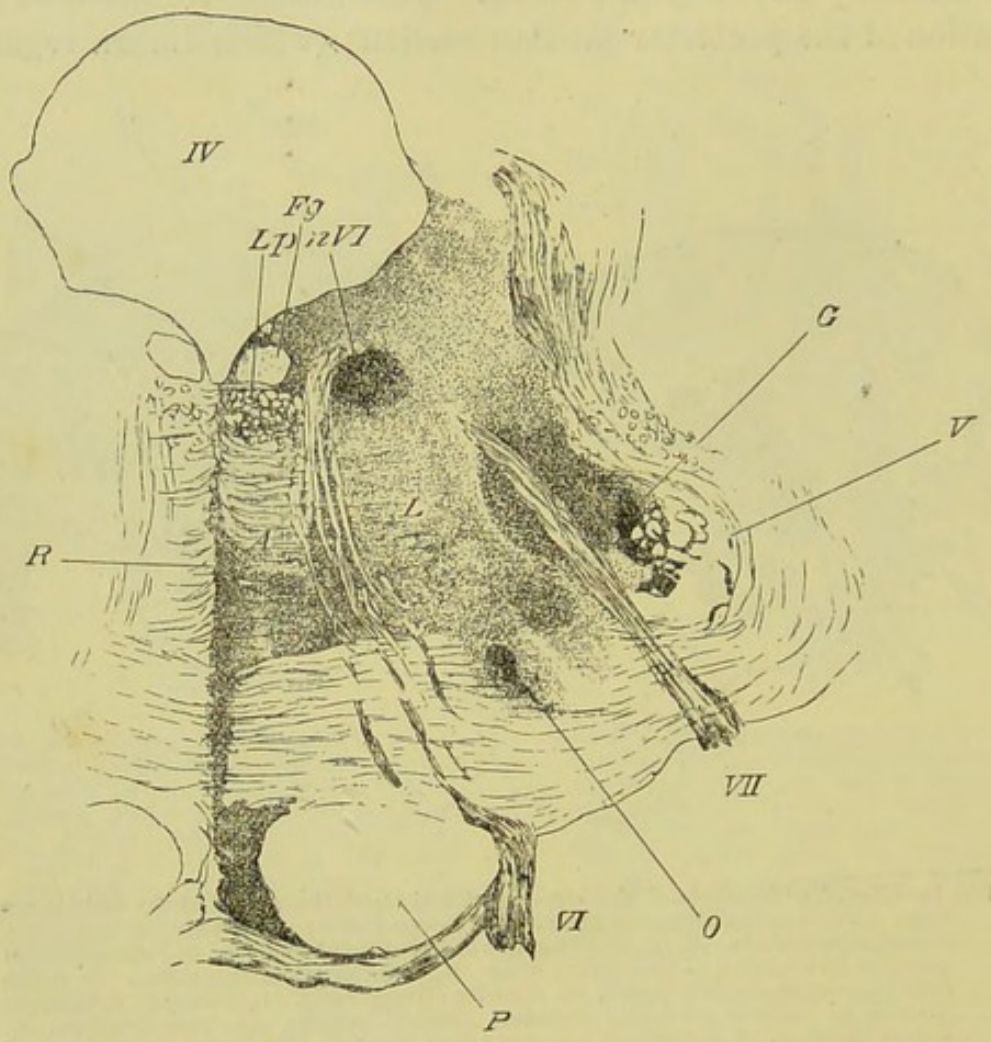


FIG. 15.—Section through Medulla Oblongata of Monkey at emergence of Sixth Nerve. (From preparation and drawing by Bevan Lewis).—A, anterior column. *Fg*, genu of facial nerve. G, substantia gelatinosa. L, lateral column. *Lp*, posterior longitudinal bundle. O, superior olivary body. P, pyramid. R, raphe. IV, fourth ventricle. V, ascending roots of fifth nerve. VI, root of abducens. *n*VI, abducens nucleus. VII, roots of facial.

and apparently specially related to some of the fibres of the auditory nerve, forming what is usually termed the anterior root, is regarded by Onufrowicz as really a formation homologous with the ganglia of the posterior spinal roots. The real origin of the anterior division (the vestibular nerve) is in the vermis cerebelli or in the grey matter of the fourth

ventricle, ventral to the superior cerebellar peduncle. The auditory nerve proper, the cochlear or posterior division, arises mainly from the tuberculum acusticum, but its connection with higher centres is not known with any degree of accuracy.

The sixth nerve (abducens oculi) springs from a nucleus close to the middle line, which is practically a prolongation upwards of the motor column, which gives origin to the hypoglossal (figs. 12 and 13, VI ; and fig. 15, *n* VI).

The seventh nerve, however (the facial), though a purely motor nerve does not spring from the ventral column, but from a nucleus occupying a position which corresponds to the detached cells of the anterior horn in the formatio reticularis. To reach this nucleus the fibres of the seventh nerve make an acute bend (knee) round the nucleus of the sixth (fig. 13, G*f*), with which, it has been supposed, also the seventh enters into relation. From a similar group of cells above the facial nucleus springs the motor root of the fifth or trigeminal nerve (fig. 12, V). This column extends from the nucleus of the facial as high up as the entrance of the aqueduct of Sylvius. The sensory root of the fifth is in part derived from a nucleus which lies laterally to the motor root (fig. 12, V′), but mainly from the caput cornu posterioris, extending from the tubercle of Rolando for a considerable distance down the cervical region, as far as the second or third segment (figs. 12, 13, V″; and figs. 11, 14, and 15, V). Some sensory roots have also been traced into the cerebellum. A considerable centre of origin of the fifth nerve is a group of large vesicular cells which surround the aqueduct of Sylvius (fig. 16, V). The roots derived from this nucleus have been described by Meynert and others as sensory, but Henle and Forel consider that they belong to the portio minor or motor division of the fifth.

The various nuclei described are connected commissurally, and with strands, crossing in their ascent, proceeding to the cerebrum. But the various paths have not been ascertained with any degree of certainty. A relationship of special importance, however, has been ascertained by Duval and Laborde. A direct connection exists between the nucleus of the sixth and certain fibres of the third and fourth cranial nerves of the opposite side. This is established through specially differentiated

tracts, which occupy the dorsal aspect of the formatio reticularis, and are termed the *posterior longitudinal bundles* (figs. 15, L *p*, 16, L). In these bundles also probably run fibres which associate other motor nuclei with each other, as they maintain a constant relation to the ventral, or motor, column of the grey matter of the fourth ventricle, and its continuation upwards in the pons.

§ 7. In the pons Varolii the ascending longitudinal tracts are traversed by the fibres of the middle peduncles of the

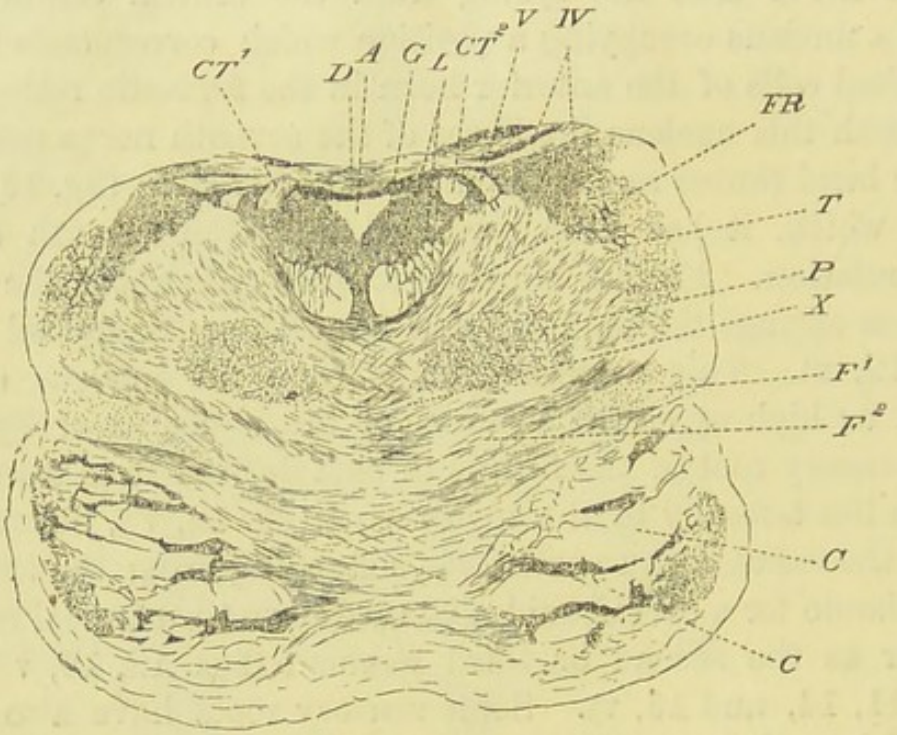


FIG. 16.—Section of Pons of Monkey in the region of the valve of Vieussens. (From preparation and drawing by Bevan Lewis).—A, aqueduct of Sylvius. C, pyramidal tracts. CT¹, roots of fourth nerve ascending to its nucleus. CT², the same seen in transverse section. D, decussation of the fourth nerves. F¹, inferior lamina of fillet (pes). F², median lamina of fillet. G, central grey substance. L, posterior longitudinal bundles. P, superior cerebellar peduncle decussating with its fellow at X. T, portion of testis. IV, fourth nerve. V, descending root of fifth nerve.

cerebellum, which form a superficial and deep layer, interweaving in the median line or raphe. The pyramidal strands are divided into separate groups or loculaments by the transverse fibres, and numbers of large multipolar cells occupy the interstices (fig. 16, c). In some animals the deep fibres of the pons are visible at the upper border of the pyramids, constituting what is called the trapezium (fig. 9, *t*). It is evident, from the greater sectional area of the pyramidal tracts in the pons, than in the medulla oblongata, that they here receive a

large accession of fibres, derived both from the nuclei of this region and from the cerebellum. It is doubtful whether there is any direct passage of cerebellar fibres into the pyramidal tracts. It is probable that the connection between the cerebellar peduncles and the pyramidal strands is established indirectly through the multipolar cells of the pons (*nucleus pontis*).

The anatomical investigations of Meynert, confirmed by pathology, show that the connection between the pyramids and cerebellar peduncles is a crossed one, i.e. the left peduncle being related to the right pyramid, and the right peduncle to the left pyramid. Hence the cerebellar lobes are in relation with the pyramidal tracts on the same side of the spinal cord, seeing that the pyramidal tracts decussate more or less completely at the lower aspect of the medulla oblongata.

Numerous other arcuate fibres exist in the pons in addition to those above mentioned, but their relations are still very imperfectly determined.

§ 8. Leaving for the present the posterior region or tegmentum, and following the course of the pyramidal tracts, we find that from the anterior aspect of the great transverse system of the pons, they emerge in the base or *foot* of the cerebral peduncles, or *crura cerebri* (fig. 7, P).

The crura cerebri diverge from each other slightly in their course upwards, and disappear into the base of the cerebral hemispheres (fig. 17). On the posterior aspect of the crura cerebri, and immediately in front of the cerebellum, are situated the *corpora quadrigemina* (in mammals) or corpora bigemina or optic lobes (in birds, frogs, and fishes) (figs. 43–45 B). The anterior pair of tubercles are termed the *nates*, and the posterior pair the *testes* (fig. 18, N and T).

These ganglia lie between the cerebellum and the optic thalami with which they appear to be respectively connected. The connection with the cerebellum is through the superior peduncles of the cerebellum or *processus a cerebello ad testes* (fig. 8, 5; fig. 18, *p s*). They extend superficially between the anterior aspect of the cerebellum and the posterior margin of the testes, and between the two is a thin transverse lamina called the *valve of Vieussens* (fig. 18, V V).

The superior cerebellar peduncles in reality pass underneath the ganglia of the corpora quadrigemina, and converge and decussate through a group of cells lying on each side of the middle line underneath the anterior tubercles of the corpora quadrigemina. These cell groups constitute each the red nucleus or *nucleus tegmenti* (fig. 19, R N). The red nucleus seems to be the primary terminus of the superior cerebellar

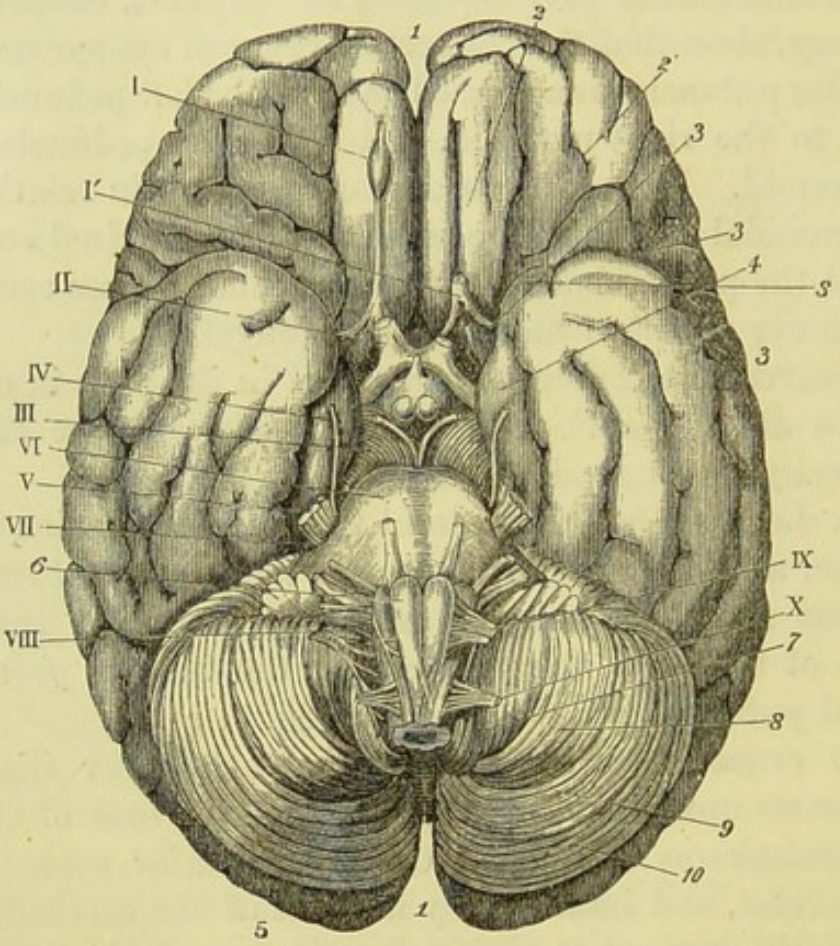


FIG. 17.—Base of the Brain. 1, superior longitudinal fissure. 2, the fissure of the left olfactory tract, which is cut. 2′, the orbital lobe. 3, 3, 3, the fissure of Sylvius. 4, the gyrus hippocampi. *s*, the subiculum cornu Ammonis. 5, the occipital lobe. 6, the anterior pyramid of the medulla oblongata. 7, the amygdaloid lobule of the cerebellum. 8, the biventral lobe. 9, the slender lobe. 10, the posterior inferior lobe. The Roman numerals I to IX indicate the respective cranial nerves; X is the first spinal nerve.

peduncle, but beyond this the fibres have been variously traced. Flechsig traces them to the lenticular nucleus (fig. 23), and also through the optic thalamus into the *corona radiata*.

Passing into the base of the corpora quadrigemina between the superior and middle peduncles of the cerebellum a tract of fibres is seen (fig. 7, 6), whose course is almost transverse to the longitudinal strands of the crus. This is the fillet or

lemniscus. These fibres come from a tract which on cross section of the pons (fig. 16, F¹, F²) is seen to form the ventral aspect of the reticular formation posterior to the pyramidal tracts. This more or less differentiated layer of the reticular formation is a continuation of the anterior and lateral root zones of the spinal cord. The relations of the fibres forming the fillet have been differently described by different anatomists.

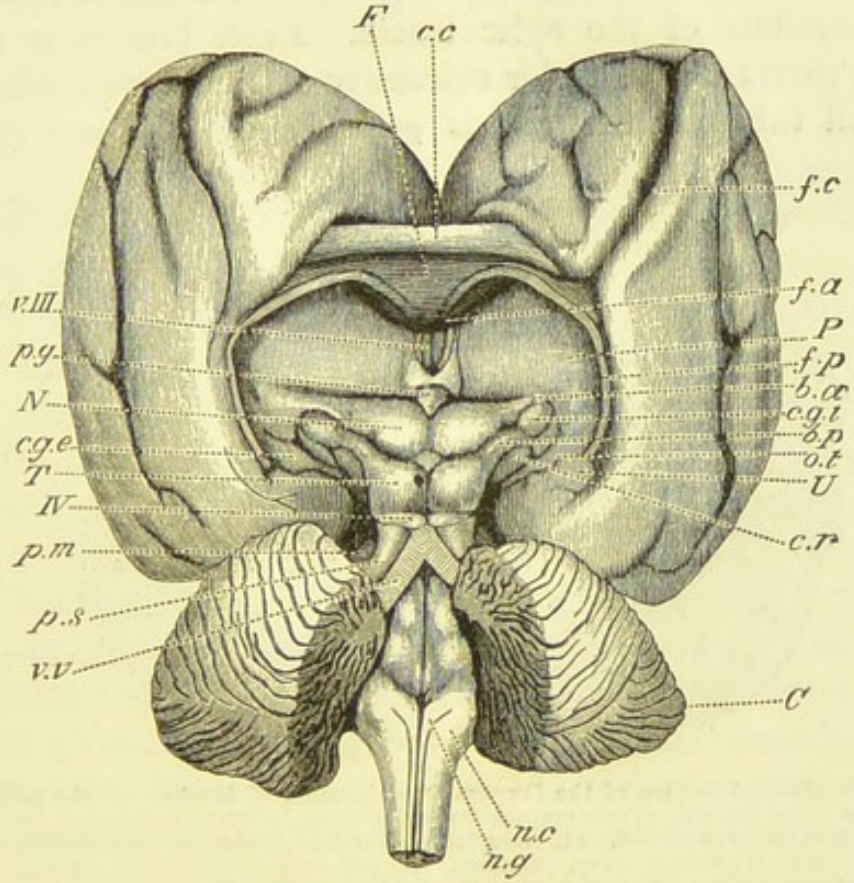


FIG. 18.—Brain of Monkey, the Cerebral Hemispheres being pushed upwards and forwards and drawn asunder, so as to expose the basal ganglia. (From a drawing by F. Lemaistre).—*ba*, brachium anterius. *bp*, brachium posterius. C, cerebellum divided in the middle line. *cc*, corpus callosum. *cge*, corpus geniculatum externum. *cgi*, corpus geniculatum internum. *cr*, crus cerebri. F, fornix. *fa*, anterior pillar of fornix. *fp*, posterior pillar of fornix. *fc*, calcarine fissure. N, nates. *nc*, nucleus cuneatus. *ng*, nucleus clavatus. *ot*, optic tract. P, pulvinar of optic thalamus. *pg*, pineal gland. *pm*, middle peduncle of cerebellum. *ps*, superior peduncle of cerebellum. T, testes. U, uncus gyri hippocampi. VV, valve of Vieussens. V.III, third ventricle. IV, roots of fourth nerve.

Meynert terms those which lie most external the lower fillet or foot of the fillet (fig. 16, F¹), and traces them to the testes. The middle or chief part of the fillet he terms the upper fillet (fig. 16, F²). These he traces to the nates. The mesial fibres he traces to certain bundles which appear to pass from the crus cerebri into the origin of the locus niger and tegmentum

(*ped. subst. nigræ*). Flechsig includes in the fillet a large bundle of longitudinal tracts ascending from the interolivary layer into the lenticular nucleus (*ansa lenticularis*), and a smaller bundle, which he terms the upper fillet, and which he traces into the fibres of the tegmentum (Haubenstrahlung). From the tubercles of the corpora quadrigemina spring the arms, or *brachia*. Those from the anterior pair are termed the anterior brachia (fig. 18, *b a*), and are more or less direct continuations of the optic tracts. Each brachium can be traced round the posterior extremity of the optic thalamus to a small tubercle, the *corpus geniculatum externum* (fig. 18,

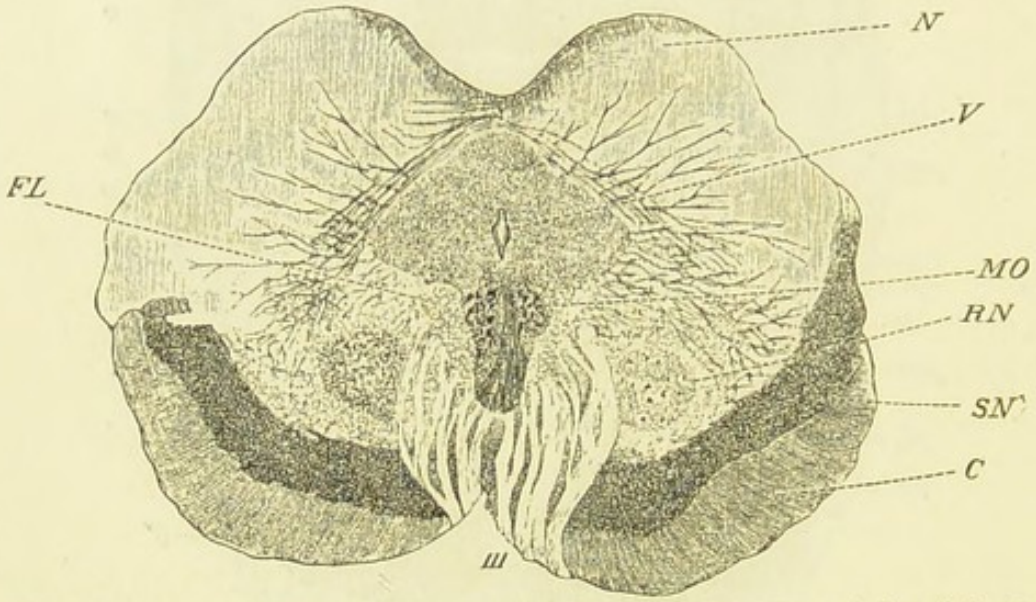


FIG. 19.—Frontal Section of the Corpora Quadrigemina of Monkey—at the origin of the Third Nerves. (From preparation and drawing by Bevan Lewis).—C, crusta, or foot of the crus cerebri. FL, posterior longitudinal fasciculus. MO, nucleus of the motor oculi or third nerve. N, nates. RN, red nucleus or nucleus tegmenti. SN, substantia nigra or locus niger. V, aqueduct of Sylvius surrounded by central grey substance. III, roots of third nerve.

c g e), and thence into the optic tract (fig. 18, *o t*, and fig. 7, II). The brachia of the posterior tubercles pass directly forward, and appear to end in two small tubercles placed somewhat external to the tubercles above mentioned and termed the *corpora geniculata interna* (fig. 18, *c g i*). The optic tracts seem to be connected with these tubercles also, but there is no real passage of fibres from the optic *nerve* into them (§ 21).

§ 9. When a section is made transversely to the crura cerebri the corpora quadrigemina have the appearance of a bridge, or arch, over a canal which is continuous with the fourth ventricle below, and the third ventricle above. This

canal, which is the remnant of that portion of the embryonic cerebro-spinal tube termed the mesencephalon, has received the name of the aqueduct of Sylvius, or *iter a tertio ad quartum ventriculum* (fig. 19, v).

The quadrigeminal arch is composed of grey matter interlaced with fibres of the brachia and arcuate fibres of the fillet which decussate above the aqueduct of Sylvius, and also of fibres which connect the corpora quadrigemina with the hemispheres.

Round the canal is the central grey substance, at the periphery of which is a layer of large vesicular cells which give origin to one of the roots of the fifth nerve (fig. 16, v). Situated ventrally to the canal on each side of the middle line are the nuclei of origin of the third or oculo-motor nerves (fig. 19, M O). Somewhat posterior and external to these cell groups are situated the nuclei of the fourth or trochlear nerves. These arise superficially from the valve of Vieussens just posterior to the testes. In the valve the respective nerves decussate with each other (fig. 16, D) in order to reach the nucleus of the opposite side. In close relation with these nuclei are seen the posterior longitudinal bundles (fig. 19, F L), which, as before mentioned (p. 23), connect the nuclei of the sixth nerves with the oculo-motor and trochlear nerves.

The great mass of the crura, between the quadrigeminal arch and the foot of the crus (fig. 19, c), is the continuation of the tegmentum, formed by the longitudinal bundles of the reticular formation and fillet, together with the fibres from the superior cerebellar peduncles decussating into the red nuclei. The red nucleus, or *nucleus tegmenti* (fig. 19, R N), occupies the middle of the tegmentum, beneath the anterior tubercle of the corpora quadrigemina, and contains numerous pigmented multipolar cells. They are traversed by the roots of the third nerve, which, however, do not appear to form connections with them. As already mentioned (p. 26), the red nuclei are the primary terminations of the superior peduncles of the cerebellum, and have been found to undergo atrophy with them.

Between the foot of the crus and the tegmentum there is a region of a semilunar shape which, owing to its containing

darkly pigmented cells, has an almost black appearance, and is known as the *locus niger* (fig. 19, S N).

The foot of the crus (fig. 19, c) forms the ventral aspect of the cerebral peduncle below and external to the locus niger. In this region ascend the pyramidal tracts which have already been traced upwards from the spinal cord, medulla oblongata, and pons.

§ 10. Before following the tracts of the crura cerebri upwards into the cerebrum it will be convenient to return to the cerebellum, the peduncles of which have already frequently been referred to. The cerebellum is a development of the posterior wall of the hindermost (metencephalon) of the three primary dilatations of the embryonic cerebro-spinal tube.

The remnant of the original cavity constitutes the fourth ventricle, which is continuous, underneath the cerebellum, on the posterior aspect of the pons with the cavity of the mesencephalon, or aqueduct of Sylvius.

The cerebellum consists of a central portion or vermis, and two lateral lobes or hemispheres, which vary greatly in size in different animals. Both the central and lateral lobes are divided into numerous secondary divisions or lobules, which have received special names (fig. 20). The interior is composed of a central stem of medullary fibres corresponding to the vermis, with radiations into the lateral lobes. The surface of the medullary radiations is covered with grey matter disposed in laminated folds. A section of the cerebellum crossing the direction of the laminæ has a beautiful pinnatifoliate appearance, and hence called *arbor vitæ* (fig. 20).

In the centre of the medullary stem of each lateral lobe of the cerebellum there is a collection of grey matter, somewhat similar to the olivary body of the medulla oblongata, termed the *corpus dentatum*; and near this are certain other detached cell groups (*nucleus emboliformis*, *nucleus globosus*). In the medullary stem of the vermis, immediately overlying the fourth ventricle, there is also a cell group, termed the *nucleus fastigii*.

Into the medullary substance and its cell groups, and thence more or less directly into the cortical substance, are traceable the peduncles of the cerebellum already described.

The inferior peduncles or restiform tracts have been followed to the cortex, and partly to the dentate nuclei. The internal division of the restiform tract is traced by Meynert to the nucleus fastigii of the same, and also of the opposite side, and thence to the upper and lateral parts of the cortex. Into the nucleus fastigii also the cerebellar root of the auditory nerve is said to pass. The middle peduncles of the cerebellum radiate directly through the medullary substance into the cortex. The superior peduncles are connected with the dentate nuclei, and through these indirectly with the cerebellar cortex.

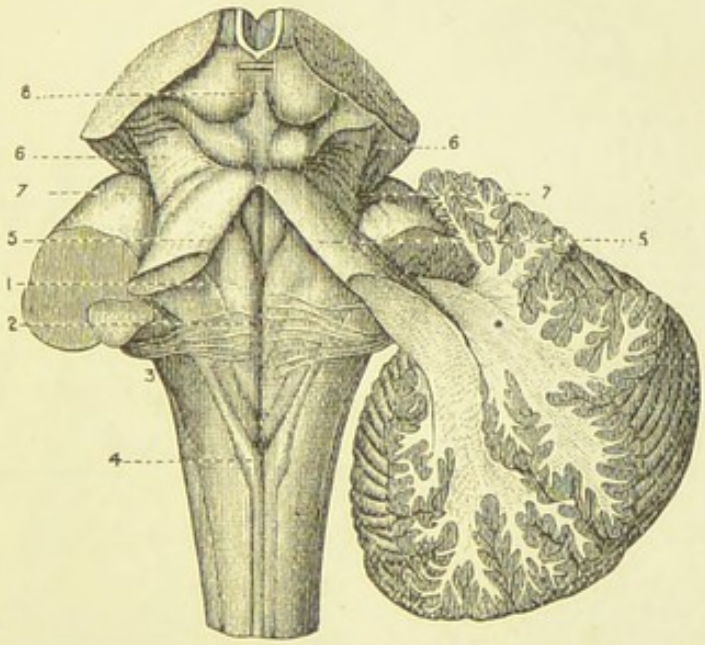


FIG. 20.—The Fourth Ventricle exposed by Division of the Cerebellum (Sappey).—On the left side the cerebellar peduncles have been cut short; on the right the middle peduncle has been cut short, while the superior and inferior retain their connections. 1, Median groove of the med. obl. bounded on each side by the *fasciculi teretes*. 2, striæ acusticæ. 3, inferior cerebellar peduncle or restiform body. 4, clavate nucleus. 5, superior cerebellar peduncle, or processus a cerebello ad cerebrum. 6, fillet. 7, crura cerebri. 8, corpora quadrigemina.

Besides the radiations of the cerebellar peduncles the medullary substance contains fibres which appear to associate different parts with each other, and commissural fibres between the lateral lobes.

The cortical substance consists of two chief layers: (1) an inner or granular layer, (2) an outer or grey layer, with (3) an intermediate cellular layer.

The inner or granular layer is composed of a dense aggregation of granules of which there are two kinds, glia cells and

ganglion cells, embedded in a plexus or network of fine fibres continuous with those of the medullary substance.

External to the granular layer, and at the boundary between it and the outer layer, is a single row of large pear-shaped cells termed the cells of Purkinje. From the base of each cell

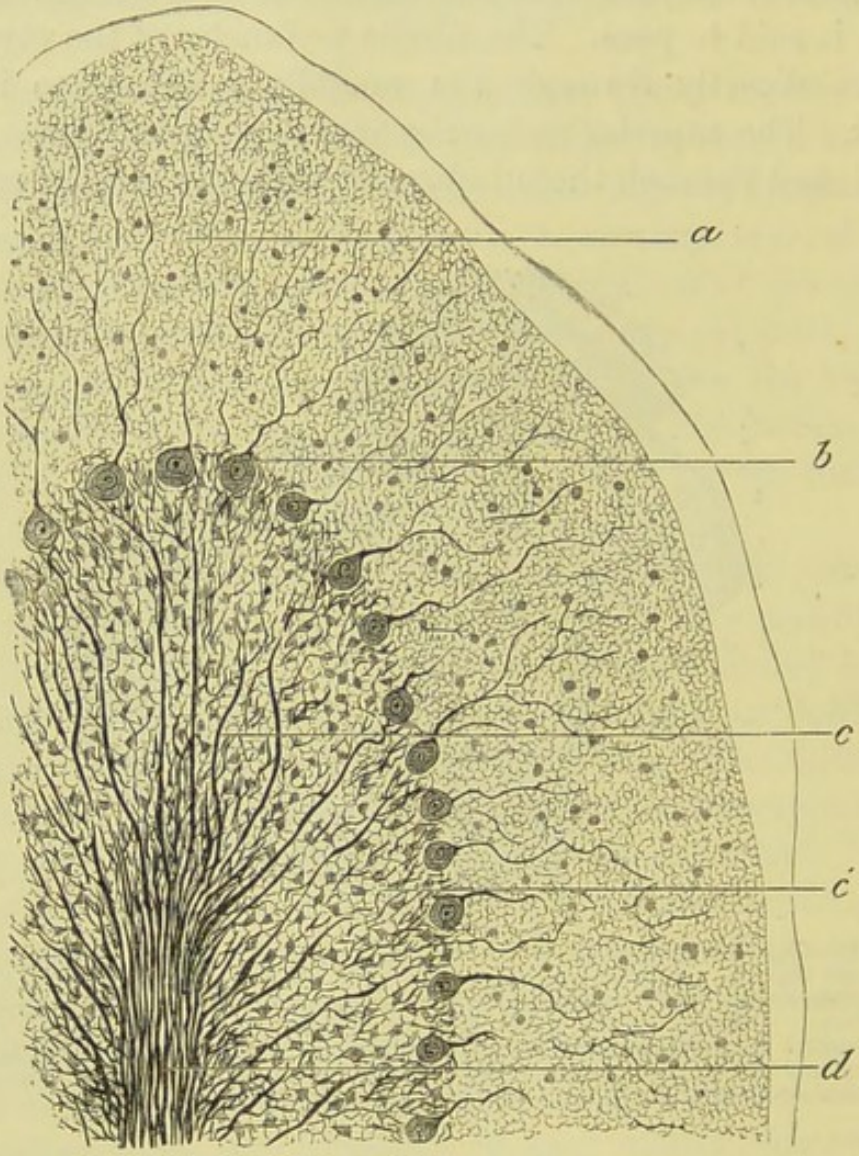


FIG. 21.—Section of a lobule of the Cerebellum (Beevor).—*a*, molecular layer, with glia cells and protoplasmic processes of Purkinje's cells. *b*, Purkinje's cells. *c*, granular layer, showing glia cells and ganglion cells with unbranched medullated fibres joining Purkinje's cells. The 'granules' are embedded in a fine network of branched medullary fibres. *d*, medullary centre.

springs a process which is directed inwards towards the granular layer, and which is continuous with a medullary fibre which passes straight through the network and granules of the inner layer (Beevor). From the outer pole spring a number of processes, which branch outwards in the outer layer. These

processes bend backwards (Obersteiner), and probably end ultimately in the fine plexus of the granular layer (Beevor).

The outer or grey layer consists of a fine matrix, in which are various elements, in addition to the branching processes of Purkinje's cells. Some appear to be only connective tissue corpuscles, while others belong to nervous tissue proper.

§ 11. The crura cerebri, which are embraced by the optic tracts in their course to the chiasma, enter the base of the

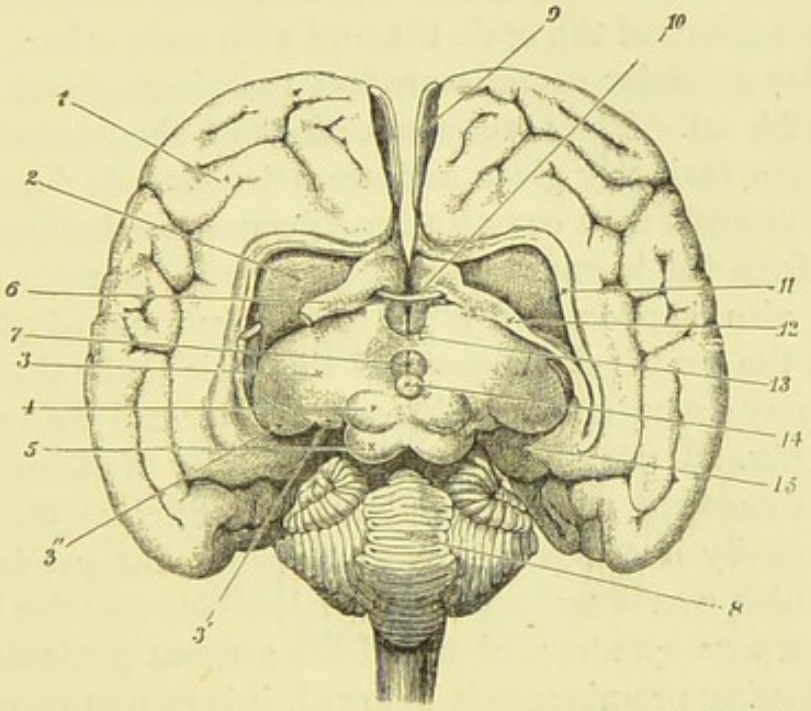


FIG. 22.—The Cerebral Hemispheres of the Dog separated after Division of the Corpus Callosum, so as to expose the Ventricles and Basal Ganglia. 1, the internal surface of the left hemisphere. 2, the corpus striatum. 3, the optic thalamus. 3′, corpus geniculatum internum. 3″, corpus geniculatum externum. 4, the nates, or anterior tubercles of the corpora quadrigemina. 5, the testes, or posterior tubercles. 6, the anterior pillar of the fornix, which is divided on the left, undivided on the right side (12). 7, the third ventricle, exposed by drawing the optic thalami asunder. 8, the upper surface of the cerebellum. 9, the olfactory bulb or rhinencephalon. 10, the anterior commissure. 11, the corpus callosum divided. 13, the soft commissure. 14, the pineal gland, situated over and concealing the posterior commissure. 15, the descending cornu of the lateral ventricle.

cerebral hemispheres, the posterior division or tegmentum into and beneath the optic thalamus, where it is called the subthalamic region, and the foot or base outside the optic thalamus into and through the divisions of the corpora striata.

The optic thalami and corpora striata are the ganglia of the base, and are only visible when the cavity of the hemispheres has been laid open by division of the corpus callosum (fig. 22), or when the hemispheres are drawn asunder and pushed upwards and forwards (fig. 18).

The optic thalami are posterior to the corpora striata and immediately anterior to the corpora quadrigemina.

Viewed from above, the optic thalami appear as two convex masses separated from each other by a space or cavity termed the third ventricle, which is continuous with the aqueduct of Sylvius, and which is prolonged downwards in the infundibulum as far as the pituitary body (fig. 7, *t c*, *h*).

The posterior margin of the third ventricle is bridged over by the posterior commissure, which seems to connect the posterior regions of the optic thalami with each other.

On the posterior commissure lies the pineal gland (fig. 18, *p g*; fig. 22, 14). The exact connections of the posterior commissure are variously given and are not definitely determined. Meynert regards it as constituting a decussation between fibres passing from the tegmentum to the optic thalamus; and this view is also supported by the investigations of Spitzka.[1] Between the ventricular aspects of the optic thalami stretches a broad grey commissure, easily torn, and termed the soft commissure (fig. 22, 13). The anterior extremity of the optic thalamus is somewhat rounded—*tuberculum anterius*; posteriorly and externally it swells into a prominence, the *pulvinar* (fig. 18, P), which overhangs and more or less conceals the brachia of the corpora quadrigemina and the corpora geniculata. If this projecting prominence is followed, it is seen to curve round and embrace the crus cerebri and to become continuous with the external geniculate body and the optic tract (fig. 18, *o t*).

Just in advance of the anterior tubercles of the optic thalami are two tracts or pillars—the anterior pillars of the fornix (fig. 18, *f a*)—which appear to descend perpendicularly towards the base; and crossing them transversely is a commissure—the anterior commissure (fig. 22, 10), to be afterwards described.

§ 12. The *corpus striatum* (fig. 22, 2) lies anterior and external to the optic thalamus. Only a portion of this ganglion is visible in the cavity of the hemisphere. This portion is termed the intraventricular ganglion, or *nucleus caudatus*. The head is situated anteriorly, but it is prolonged like a tail ex-

[1] *Neurolog. Centralblatt*, No. 11, June 1, 1885. On this see also Chap. V. p. 158, note.

ternally to the optic thalamus, and follows the course of the descending cornu of the hemisphere as far as the extremity of the temporal lobe (fig. 22, 15).

The other portion of the corpus striatum—the extraventricular nucleus, or *nucleus lenticularis*—is only seen when sections are made through the hemisphere (figs. 23, 24, *n l*). The posterior division of the crus cerebri or tegmentum is continued beneath the optic thalamus as the subthalamic region, the foot of the crus is continued upwards into the internal capsule (fig. 23, *i c*).

When a section is made of the cerebral hemispheres at right angles to the crura cerebri, the relative position of the optic

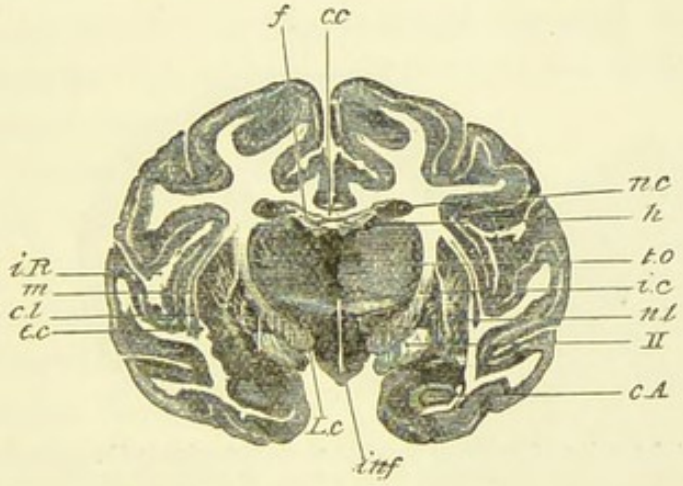


FIG. 23.—Frontal Section of Brain of Monkey—at right angles to Crura Cerebri (nat. size).—CA, cornu Ammonis at anterior extremity of descending cornu of lateral ventricle. *cc*, corpus callosum. *cl*, claustrum. *ec*, external capsule. *f*, fornix. *h*, tænia. *ic*, internal capsule. *inf*, infundibulum. IR, island of Reil. LC, Luys' body, or corpus subthalamicum. *m*, medullary lamina. *nc*, nucleus caudatus. *nl*, nucleus lenticularis. II, optic tract.

thalamus, nucleus caudatus, nucleus lenticularis, and internal capsule is distinctly displayed. The internal capsule (fig. 23, *i c*), into which the foot of the crus enters, has a somewhat semilunar shape, and ascends external to the optic thalamus, embracing this and the subthalamic region in its concavity, and having the lenticular nucleus on its convex aspect.

§ 13. The foot of the crus contains the fibres of the anterior pyramids and pyramidal tracts of the spinal cord; but, as has already been mentioned, it is evident, from the greater sectional area of the foot as compared with the anterior pyramids, that other tracts also ascend in this posi-

tion. The pyramidal tract proper occupies the middle third or half of the crus (fig. 19, c).

The outer third has been regarded by Meynert and Huguenin as the continuation of the posterior columns of the spinal cord (see p. 18), but this is denied by Flechsig. Flechsig considers them to be continuous with certain dorso-lateral tracts of the pons, but their further relations are not clear. He thinks they are continued into the cerebellum, but, as will be afterwards shown, this cannot be accepted.

The inner third of the foot of the crus—the accessory pyramidal tract—contains the fibres which probably have the same relation to the motor nuclei of the medulla, pons, &c. as the pyramidal tract to the anterior horns of the spinal cord.

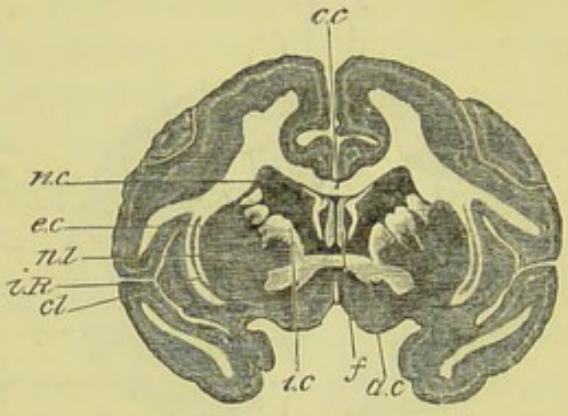


FIG. 24.—Frontal Section of Brain of Monkey at right angles to the crura cerebri, in the region of the anterior commissure (nat. size).—*ac*, anterior commissure. *cc*. corpus callosum. *cl*, claustrum. *ec*, external capsule. *f*, pillars of fornix. *ic*, internal capsule. *iR*, island of Reil. *nc*, nucleus caudatus. *nl*, nucleus lenticularis.

Certain fibres which are in immediate relation with the locus niger ascend with the other fibres of the foot of the crus into the internal capsule.

The lenticular nucleus has a triangular shape, the base directed outwards towards the island of Reil. It consists of three divisions, separated by medullary laminæ (fig. 23, *n l*).

The basal division is separated from the cortex and medullary fibres of the island of Reil by a thin strip of grey matter, the *claustrum* (fig. 23, *cl*), and by a thin layer of fibres termed the *external capsule* (fig. 23, *e c*).

Beneath the optic thalamus, and embraced in the concavity of the internal capsule, is the subthalamic region, in which is a cell group which bears the same relation to the internal capsule as the locus niger to the foot of the crus.

This group of cells constitutes Luys' body, or *corpus subthalamicum* (fig. 23, L *c*).

Frontal sections in this region show only the tail of the nucleus caudatus (fig. 23, *n c*) lying at the upper external aspect of the optic thalamus, separated from the lenticular nucleus by the internal capsule.

But in sections farther forwards (fig. 24) the area of the caudate nucleus increases, while that of the lenticular nucleus diminishes, until at the anterior extremity the internal capsule is seen to be embraced by the two divisions of the corpus striatum, more or less fused with each other, showing that the lenticular and caudate nuclei are merely divisions of essentially one ganglion.

When a horizontal section is made through the middle of the basal ganglia (fig. 25) the relations of the internal capsule to the corpus striatum and optic thalamus are displayed in a different aspect.

The internal capsule with its fellow of the opposite side has an X-shaped appearance—the anterior half, situated between the nucleus caudatus and nucleus lenticularis, forming, with the posterior half, situated between the optic thalamus and nucleus lenticularis, a sharp angle or *knee* (fig. 25, *i c*). The other structures visible in frontal sections are readily recognisable in their same relative positions.

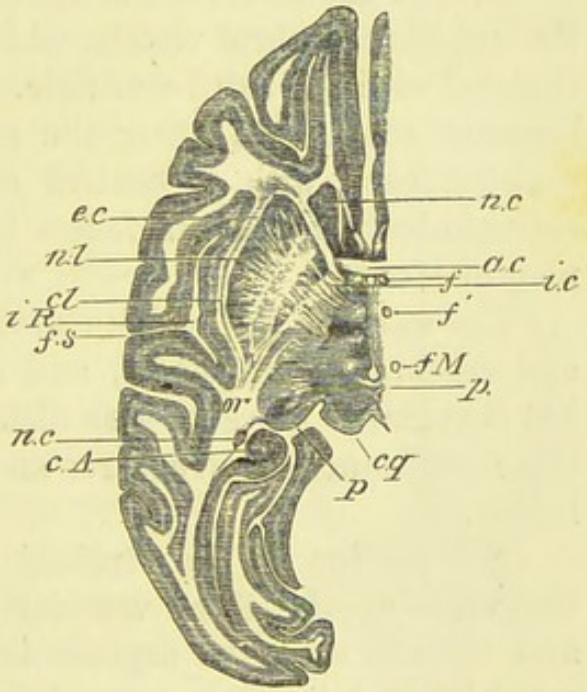


FIG. 25.—Horizontal Section of Left Hemisphere of Monkey—on a level with the anterior commissure (nat. size).—*ac*, anterior commissure. CA, cornu Ammonis. *cl*, claustrum. *cq*, corpora quadrigemina. *ec*, external capsule. *ic*, internal capsule. *in*, island of Reil. *f*, anterior or descending (Meynert) pillar of fornix. *f'*, ascending fibres, or Vicq d'Azyr's bundle. *fm*, Meynert's fasciculus. *fs*, fissure of Sylvius. *nc*, nucleus caudatus. *nl*, nucleus lenticularis. *or*, optic radiations (Gratiolet). P, pulvinar. *p*, posterior commissure.

Into the lenticular nucleus of the corpus striatum pass certain tracts of the foot of the crus, besides many from the tegmentum, included in what is termed the lenticular loop

(ansa lenticularis), which cross the ascending tracts of the internal capsule.

The internal capsule containing all the fibres of the foot of the crus, except those ending in the lenticular nucleus, and reinforced by fibres from the optic thalamus and subthalamic region, emerges from between the lenticular nucleus and tail of the caudate nucleus as the *corona radiata*, which spreads out in the form of a hollow fan towards the cortex of the hemisphere.

§ 14. Each hemisphere forms a kind of hollow shell enclosing and overlapping the basal ganglia. The central cavities—the lateral ventricles—communicate with each other and with the third ventricle, and through this with the rest of the cerebro-spinal canal.

These relations are best seen in the embryonic brain.

At first the cerebrum is merely a vesicular protrusion from the anterior cerebral vesicle, which ultimately forms the optic thalami with the third ventricle. The originally single vesicle becomes constricted along the middle line, so as to form two vesicles, each with a central cavity—the lateral ventricle, communicating with its fellow by a small opening, the foramen of Monro.

The walls of the vesicles develop into the corpora striata and cerebral hemispheres, and obscure the primitive form; but it remains more or less distinctly traceable, and explains the significance of structures and relations otherwise unintelligible.

The outline of the cerebral vesicles may be traced from the walls of the third ventricle. Here they are very thin, and form in man the septum lucidum, the two layers separated by an interspace termed the fifth ventricle, which, however, has none of the characters of the other divisions of the cerebro-spinal tube, and has no communication with them. The walls of the septum lucidum are much thicker relatively in other animals, and show the essential structure of the rest of the hemispherical wall (fig. 22, in front of 10). From the septum lucidum the wall of the hemisphere may be traced continuously all round and back again to the extremity of the temporo-sphenoidal lobe, where it fuses with the substantia

innominata of the anterior perforated space which is continuous with the central grey matter of the cerebro-spinal tube (fig. 7, x x, and fig. 17).

The fully developed hemisphere has the shape of an irregular spherical triangle, the convexity of which is directed outwards.

The flattened mesial aspects approach each other in the longitudinal fissure, at the bottom of which is the corpus callosum (fig. 18, *c c*), or great transverse commissure, which connects the two hemispheres together. Division of this commissure exposes the interior of the hemispheres (fig. 22, 11). The cavity of each hemisphere has the general form of the exterior. The anterior extremity, which extends into the frontal region, is called the anterior horn of the lateral ventricle; the posterior extremity, which extends into the occipital region, is termed the posterior horn; and the prolongation, which dips in the direction of the temporal region, is termed the descending horn of the lateral ventricle.

§ 15. The external surface of the hemispheres is in many of the lower animals smooth (fig. 26, A), or only obscurely marked by fissures or folds, but in all the higher animals, and specially in man, the surface is disposed in folds or convolutions separated by primary and secondary fissures, or sulci, which have a definite position and relation to each other (see Chap. VIII.) At present it will suffice to indicate some of these and the great divisions which are usually made of the hemispheres.

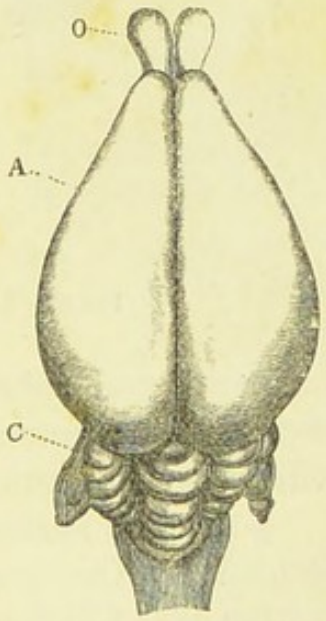


FIG. 26.—Brain of Rabbit.—A, smooth cerebral hemisphere. C, cerebellum. O, olfactory bulb.

The first and most important fissure is the fissure of Sylvius (fig. 27, A), which runs obliquely upwards and backwards from the anterior perforated space. If the edges of this fissure are drawn asunder a portion of the cortex is displayed, which is moulded over the lenticular nucleus of the corpus striatum (fig. 25). This is termed the central lobe, or island of Reil (fig. 25, *i* R; fig. 7, *c*).

The hemisphere may be considered as having been sharply bent round the upper extremity of the fissure of Sylvius into two great divisions. Above and in front of it are the frontal lobe (fig. 27, F L), and the parietal lobe (fig. 27, P L), separated from each other by the fissure of Rolando (fig. 27, B), or central fissure.

Behind and below it are the occipital lobe (fig. 27, O L), separated from the parieto-occipital fissure (fig. 27, C), and the temporal, or temporo-sphenoidal lobe (fig. 27, T S L), which is directed downwards and upwards. These names are derived from the relations which these portions of the brain have to the frontal, parietal, occipital,

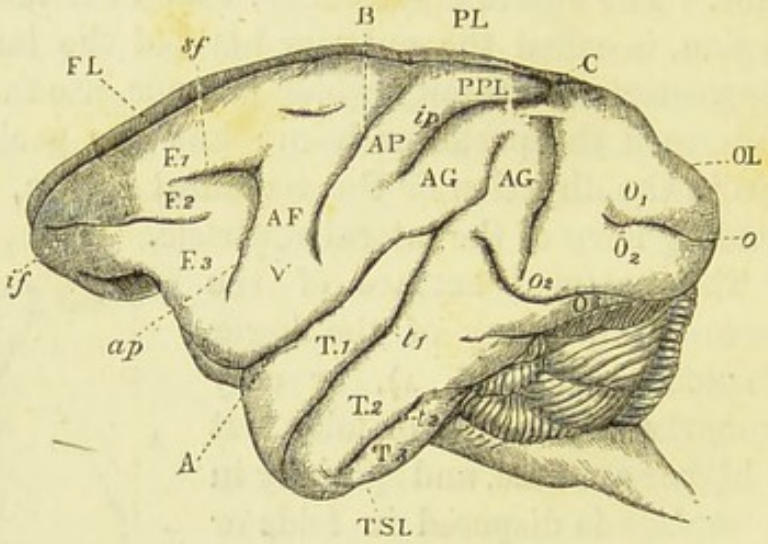


FIG. 27.—Left Hemisphere of Brain of Monkey (Macaque).

temporal, and sphenoidal bones of the skull. Each lobe is divided into numerous secondary and tertiary divisions, which will be detailed subsequently (see fig. 67 with description).

§ 16. The surface of the ridges and depths of the sulci is formed by the grey matter. The nerve cells of the grey matter are of different kinds and variously grouped, viz. small roundish and angular cells scattered almost throughout the whole cortex; spindle cells, most occurring towards the medullary aspect of the cortex; and pyramidal cells, some of which are of great size (giant cells). These elements are variously arranged and grouped in different regions of the cerebral hemispheres (see figs. 28–33). The medullary fibres penetrate the cortical grey substance to a certain depth, but the exact



FIG. 28.—Cortex of Frontal Lobe of Monkey. (× 147, Bevan Lewis.)—1, first or peripheral layer. 2, second layer, small angular cells. 3, third layer, large pyramidal cells. 4, fourth layer, ganglionic cells. 5, fifth layer, spindle cells.



FIG. 29.—Cortex of Motor Area of Brain of Monkey. (× 147, Bevan Lewis.)—1, first or peripheral layer. 2, second layer, small angular cells. 3, third layer, large pyramidal cells. 4, fourth layer, ganglionic cells and 'cell clusters.' 5, fifth layer, spindle cells.



FIG. 30.—Cortex of Temporal Lobe of Monkey. (× 147, Bevan Lewis.)—1, first or peripheral layer. 2, second layer, small angular cells. 3, third layer, pyramidal cells. 4, fourth layer, granular stratum. 5, fifth layer, ganglionic cells. 6, sixth layer, spindle cells.

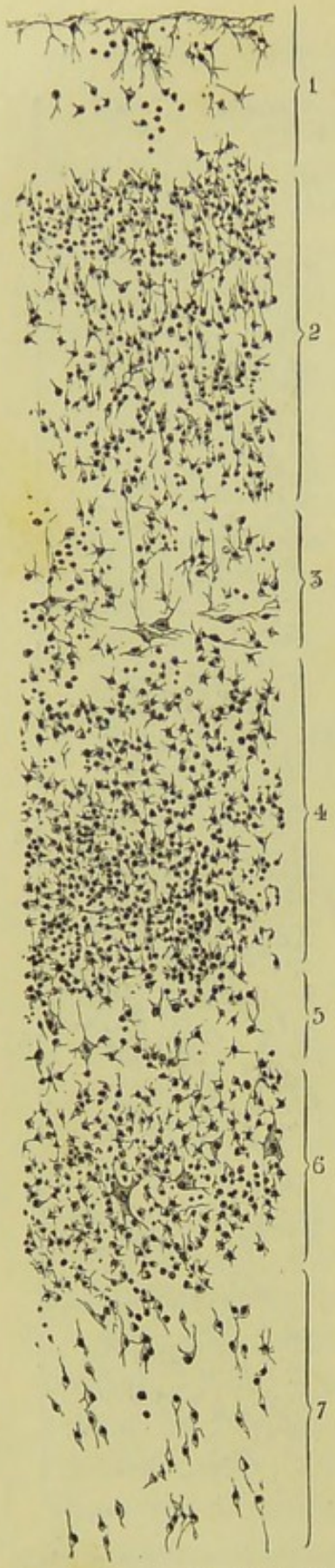


FIG. 31.—Cortex of Occipital Lobe. (× 145, Bevan Lewis.)—1, first or peripheral layer. 2, second layer, small angular cells. 3, third layer, pyramidal cells. 4, fourth layer, angular and granule cells. 5, fifth layer, pyramidal cells. 6, sixth layer, granules and ganglionic cells. 7, seventh layer, spindle cells.

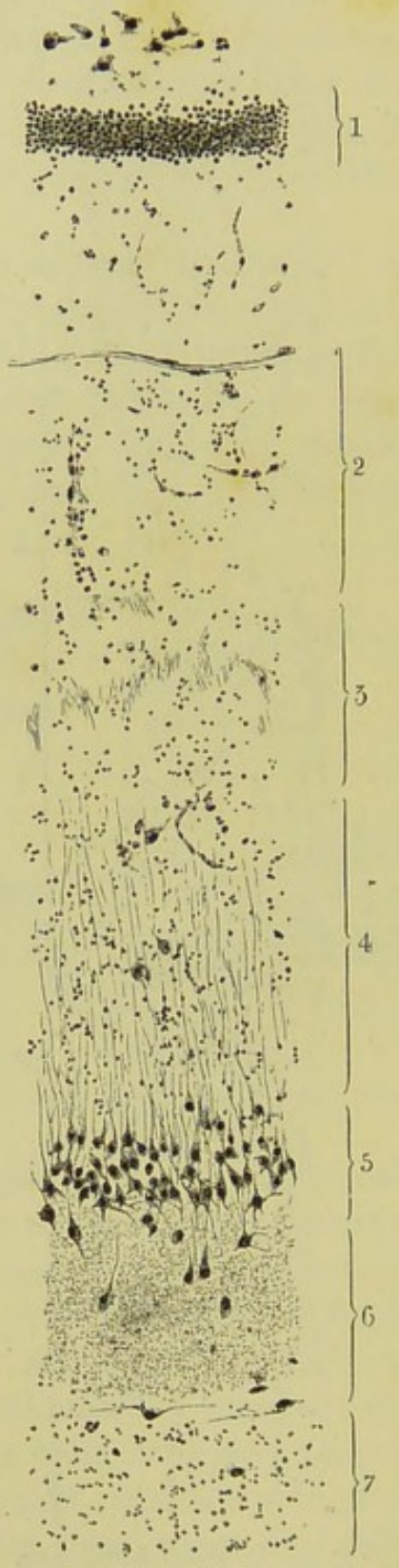


FIG. 32.—Cornu Ammonis of Monkey. (× 147, Bevan Lewis.)—1, granular stratum of fascia dentata. 2, nuclear lamina. 3, stratum lacunosum. 4, stratum radiatum. 5, ganglionic layer. 6, molecular stratum. 7, alveus.



FIG. 33.—Cortex of Gyrus Hippocampi. (× 145, Bevan Lewis.)—1, First or peripheral layer. 2, second layer, aggregated pyramidal cells. 3, third layer, large pyramidal cells.

relations of the various layers to the medullary fibres and to each other have not been as yet determined. It is supposed that the basal processes at least of the large pyramidal cells become each directly continuous with a medullary fibre, like the axis cylinder processes of the multipolar cells of the anterior horns of the spinal cord.

The grey matter of the cortex at the inner margin of the temporal lobe is folded inwards, so as to form a ridge in the descending cornu of the lateral ventricle (fig. 25, *c* A). This inverted convolution is, owing to its shape, termed the hippocampus major, or *cornu Ammonis*. It follows the course of

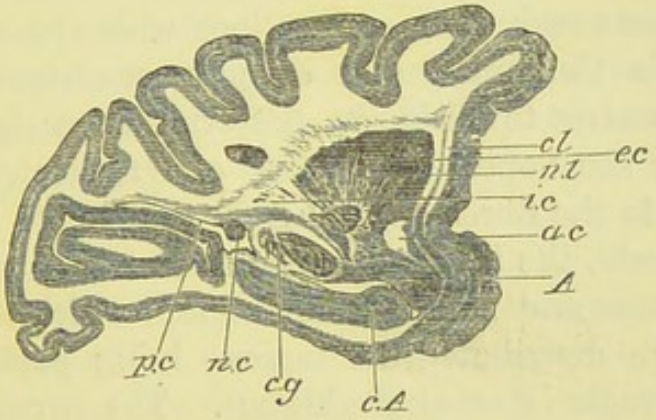


FIG. 34.—Sagittal Section of Hemisphere of Monkey (nat. size).—A, nucleus amygdalæ. *ac*, termination of anterior commissure. cA, cornu Ammonis. *cg*, corpus geniculatum externum. *cl*, claustrum. *ec*, external capsule. *ic*, internal capsule. *nc*, tail of nucleus caudatus. *nl*, nucleus lenticularis. *pc*, posterior cornu of lateral ventricle.

the descending cornu to its lower or anterior extremity (fig. 34). At this point the cortex of the temporal lobe is considerably thickened, so that on section it looks like an almond-shaped tubercle, and is termed the *nucleus amygdalæ* (fig. 34, A; fig. 36, A).

§ 17. Reverting again to the basal ganglia and internal capsule we have seen that certain of the tracts followed up from the foot of the crus terminated in the corpora striata, but that the rest of the fibres of the internal capsule passed through between the divisions of this ganglion on towards the cortex (fig. 34, *ic*). The pyramidal tract ascends in that portion of the internal capsule immediately posterior to the 'knee,' as seen in horizontal section (fig. 25, *ic*), forming the anterior third of the posterior division, and is distributed to

the cortical regions bounding the fissure of Rolando (see Chap. X.). There is thus a direct continuity between certain regions of the cortex and the pyramidal tracts of the spinal cord.

The portion of the internal capsule situated anterior to the knee or the anterior division contains those fibres of the foot of the crus situated mesially to the pyramidal tracts, and which are distributed to the frontal regions of the cortex (see Chap. X. § 24). The fibres of the outer division of the crus cerebri ascend in the posterior division of the internal capsule and bend outwards and downwards to the region of the hippocampus (Flechsig). With these ascend fibres derived from the optic tracts and their connections with the corpora geniculata, optic thalamus, and corpora quadrigemina, which spread themselves towards the posterior or occipital regions, constituting the 'optic radiations' of Gratiolet (fig. 25, *o r*). In addition to the fibres derived from the foot of the crus and the optic tracts, the internal capsule receives fibres from the optic thalamus and subthalamic region, which, according to Flechsig, are distributed to regions lying posterior to the pyramidal tracts (Haubenstrahlung). The corona radiata is composed, in addition to the fibres of the internal capsule, of fibres connecting the cortex with the optic thalamus, and, according to some anatomists, also with the divisions of the corpus striatum.

§ 18. Of the fibres from the optic thalamus a tract has been traced by Meynert from the anterior extremity towards the frontal regions. Another tract descends from the anterior extremity on its internal aspect and then passes outwards beneath the lenticular nucleus towards the regions of the island of Reil. Some of these fibres appear to be continuous with the external capsule (fig. 23, *e c*). The corpus striatum was regarded by Meynert as a 'ganglion of interruption' of the fibres connecting the cerebral cortex with the periphery. From the base of the lenticular nucleus he traced fibres of the corona radiata ascending into the frontal and parietal regions, and similarly a set of fibres connecting the cortex with the upper lateral aspect of the nucleus caudatus. This view of the relations of the corpora striata to the hemispheres,

though recently defended by Kowaleski,[1] has, however, been contested by Henle, Wernicke, and others, who maintain that neither the nucleus caudatus nor nucleus lenticularis is connected with the cortex through the corona radiata, but that these ganglia are themselves terminal stations of certain tracts of the cerebral peduncle, and are in fact only modified portions of the hemisphere, co-ordinate with, but not subordinate to, the grey matter of the cortex. This view seems to be more in harmony with the anatomical appearances than that advocated by Meynert, though we cannot regard the point as yet definitely settled.

§ 19. The cerebral hemispheres are connected together by a great system of commissural fibres, the corpus callosum (fig. 18, *cc*), which forms the floor of the longitudinal fissure and roof of the cerebral ventricles. The fibres of this system are in the middle mainly transverse, but as they enter the hemispheres they diverge in various directions—forwards, transversely, backwards, and downwards—so as to reach all the parts of the hemispheres to which the corona radiata is distributed. Owing to the appearances thus presented, it has by some been erroneously supposed that the corona radiata is merely the terminal distribution of the fibres of the corpus callosum decussating with each other in the middle line; a view which is utterly at variance with the physiology and pathology of the cerebral hemispheres.[2]

Underneath the corpus callosum and more or less fused with it (fig. 18, F) posteriorly there is another system of fibres—the fornix—which connects the hippocampi with each other and

[1] *Centralblatt f. Nervenheilkunde* (abstract), No. 3, 1883.

[2] The theory that the corpus callosum is a decussation of the fibres of the internal capsule, originally advanced by Foville, has been recently revived and more or less modified by Hamilton (*Proc. Roy. Soc.* vol. xxxvi. 1884), on the strength of the appearances presented by sections prepared and enlarged by a special method of his own (*Brain*, vol. vi. 1884). The method of investigation adopted by Hamilton—mere naked-eye appearances or lens amplification—is not competent to distinguish between apparent and real continuity of fibres and tracts with each other; and it has been shown by Beevor (*Brain*, Oct. 1885) that in sections stained (Weigert's method) so as to display the medullary fibres, and properly examined by the microscope, the fibres of the internal capsule and corpus callosum interweave with each other in proceeding to the grey matter of the cortex. There is no direct continuity between the two sets of fibres.

with the optic thalami. The fibres of this system spring, as the posterior pillars, or fimbriæ, from the free surface of the cornu Ammonis on each side. These ascend and converge and form the body of the fornix. Here many of the fibres have an almost transverse direction, constituting the appearance termed the lyra of the fornix. From the body other fibres continue forwards, gradually converging, and descend as the anterior pillars immediately behind the anterior commissure.

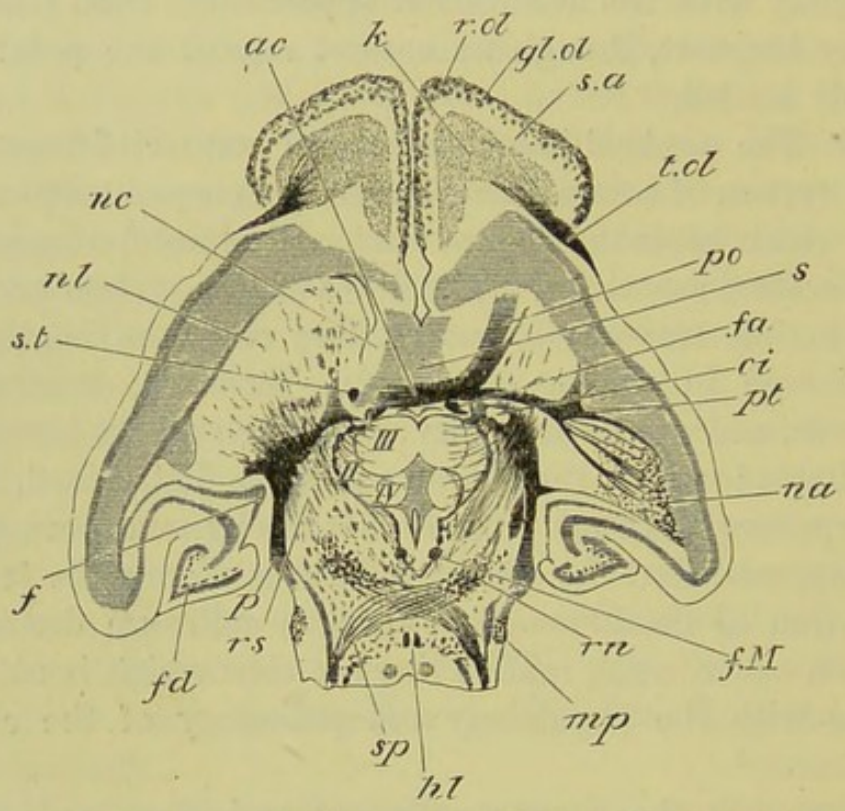


FIG. 35.—Horizontal Section of the Brain of the Mole on a level with the anterior commissure (× 4). (After Ganser.)—*ac*, anterior commissure, dividing into *po*, pars olfactoria, and *pt*, pars temporalis. *ci*, internal capsule. *f*, fimbria. *fa*, anterior pillar of fornix. *fd*, fascia dentata. *f.M*, Meynert's fasciculus. *gl.ol*, glomeruli olfactorii. *hl*, posterior longitudinal fasciculus. *k*, granular layer of olfactory bulb. *mp*, middle peduncle of cerebellum. *na*, nucleus amygdalæ. *nc*, nucleus caudatus. *nl*, nucleus lenticularis. P, pyramidal tract. *rn*, red nucleus. *r.ol*, roots of the olfactory nerve. *r.s*, regio subthalamica. *s*, septum lucidum. *sa*, substantia alba. *sp*, superior cerebellar peduncles. *st*, stria terminalis. *t.ol*, tractus olfactorius.

These descend as far as the corpora mammillaria (fig. 7, *a*), and here twisting on themselves reascend to the anterior tubercles of the optic thalami.[1]

[1] It is, however, supposed by Gudden, Forel, and others that there is no direct continuity between the descending and ascending fibres. What are here termed, with Meynert, the descending and ascending pillars are sometimes spoken of in a reverse manner, as if the corpora mammillaria were the starting-pont of the fornix. The descending pillars are therefore termed the ascending, and the ascending fibres the descending. Owing to the direct continuity of these

§ 20. The *anterior commissure*, which appears to connect the corpora striata with each other, has in reality no connection with these ganglia. The anterior commissure is composed of two divisions, which are best seen in animals which have highly developed olfactory bulbs (see fig. 35, *a c*).

The anterior division (*pars olfactoria*, *p o*, fig. 35) consists of fibres which connect the olfactory bulbs with each other. This portion of the anterior commissure is by far the larger in those animals which have large olfactory bulbs, and is inconspicuous in the monkey and man.

But in these there may be seen also fibres of this division passing from the anterior commissure downwards and forwards in the direction of the point where the inner root of the olfactory tract joins the hemisphere (fig. 24, *a c*).

The posterior division (*pars temporalis*, *p t*, fig. 35), which varies much in size in different animals, passes outwards and downwards with a curve backwards, beneath the lenticular nucleus, towards the nucleus amygdalæ and hippocampal lobule, in the medullary fibres of which it spreads out in the form of a pencil (figs. 35, 36). The whole of the fibres terminate in this region in front of the descending cornu of the lateral ventricle (see fig. 34, *a c*).

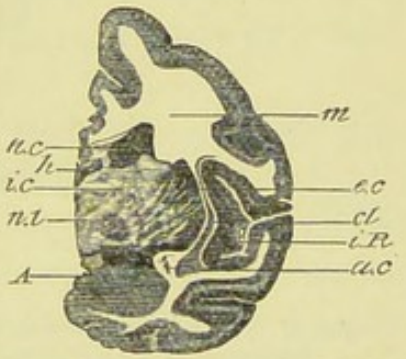


FIG. 36.—Frontal Section of Right Hemisphere of Monkey through the Nucleus Amygdalæ (nat. size). A, nucleus amygdalæ. *ac*, termination of anterior commissure. *cl*, claustrum. *ec*, external capsule. *h*, tænia semicircularis. *ic*, internal capsule. *iR*, island of Reil. *m*, corona radiata. *nc*, nucleus caudatus. *nl*, nucleus lenticularis.

No fibres pass to the occipital region, as Meynert has supposed.

Besides these commissural or associating fibres others have been described as connecting different convolutions and different regions of the cortex with each other. Some of these are more or less hypothetical and artificial; others, such as the longitudinal system of the gyrus fornicatus and gyrus hippocampi, appear to come under the category of associating fibres.

§ 21. The roots of the optic tracts have already been traced.

two sets of fibres being disputed, the fibres here termed the ascending have been termed by Forel *Vicq d'Azyr's fasciculus*.

The tracts wind round the crura cerebri and unite to form the chiasma, whence spring the optic or second cranial nerves (fig. 37, II). The constitution and mode of disposition of the respective tracts in the optic nerves are subjects on which much has been written, and will be discussed further in connection with experimental data (Chap. V.).

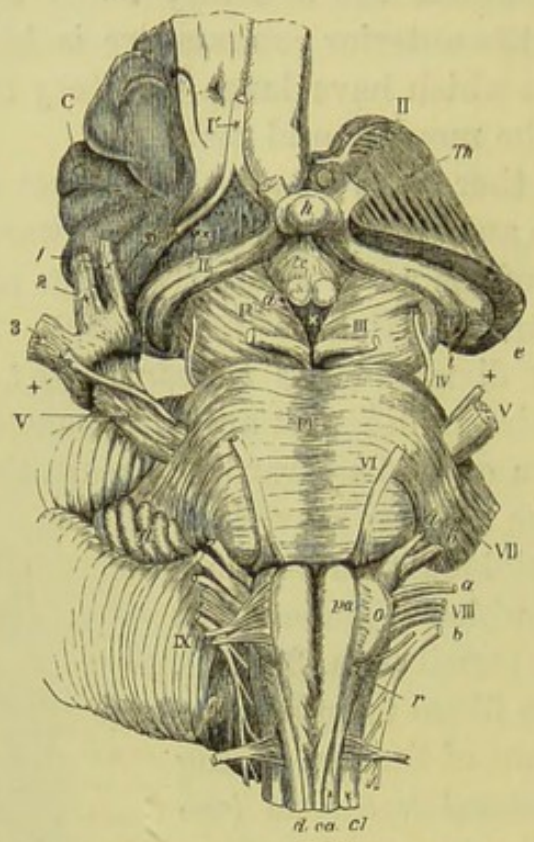


FIG. 37.—View from before of the Medulla Oblongata, Pons Varolii, Crura Cerebri, &c. (After Quain).—On the right side the convolutions of the central lobe, or Island of Reil, have been left; on the left the incision has been carried between the optic thalamus and the cerebral hemisphere. I′, the olfactory tract cut short. II, the left optic nerve in front of the commissure. II′, the right optic tract. *Th*. The cut surface of the left optic thalamus. *c*, the Island of Reil. *Sy*, the fissure of Sylvius. XX, locus perforatus anticus. *e*, the external, and *i* the internal corpus geniculatum. *h*, the hypophysis cerebri, or pituitary body. *tc*, tuber cinereum and infundibulum. *a*, one of the corpora albicantia. P, the peduncle, or crus cerebri. III, close to the left oculo-motor nerve. *x*, the locus perforatus posticus. *PV*, Pons Varolii. V, the greater root of the fifth nerve. +, the lesser or motor root; on the right side this is placed on the Gasserian ganglion. 1, 2, 3, the divisions of the fifth nerve. VI, the sixth nerve. VII *a*, the facial. VII *b*, the auditory. VIII, the pneumogastric. VIII *a*, the glosso-pharyngeal. VIII *b*, the spinal accessory. IX, the hypoglossal. *fl*, the flocculus. *pa*, the anterior pyramid. *o*, the olivary body. *r*, the restiform body. *d*, the anterior median fissure of the spinal cord, above which is the decussation of the pyramids. *ca*, the anterior column. *cl*, the lateral column of the spinal cord.

In regard to the tracts, it would appear, from the researches of Gudden on the effects of extirpation of the eyeballs, that the roots of the optic tracts which spring from the corpora geniculata interna have no real connection with vision, as they do not undergo atrophy, like the other roots, when the eyes are

destroyed. They are regarded by Gudden as forming a commissure in the posterior angle of the chiasma—the *inferior commissure*. The true roots of the optic tract are those which pass to the corpus geniculatum externum, pulvinar, and anterior brachium of the corpora quadrigemina. Stilling derives a root also from the corpus subthalamicum, or Luys' body, but this is not substantiated by the researches of Monakow.

§ 22. The olfactory or first pair of cranial nerves spring from the olfactory bulbs, which lie on the cribriform plates of the ethmoid bone. The olfactory bulbs were primarily protrusions of the cerebral vesicles, the cavity continuous with the lateral ventricles, a condition still seen in the rhinencephalon of the frog (fig. 43). In process of development the cavity becomes more or less obliterated, and the walls of the protrusion become converted into the olfactory bulb and olfactory tract, intervening between it and the hemisphere. The olfactory tract (fig. 37, 1′) is joined to the hemisphere by two apparent roots, an inner and an outer root, separated by a triangular interval in the anterior perforated space (*trigonum olfactorium*).

Between the two roots the junction with the anterior perforated space is sometimes described as a third root.

The inner root joins the mesial aspect of the anterior extremity of the gyrus fornicatus, while the outer root passes outwards across the fossa Sylvii to the extremity of the temporo-sphenoidal lobe, where it fuses with the anterior extremity of the gyrus hippocampi, subiculum cornu Ammonis, or hippocampal lobule. The termination of this root is not so evident in the monkey as in animals with very highly developed bulbs (figs. 73, 78). In these this portion of the hemisphere forms a distinct lobe or protuberance, the natiform protuberance (Owen), or pyriform lobe (Gudden), or hippocampal lobule.

The olfactory tract consists mainly of the medullary fibres of the original rhinencephalon, from which the grey matter has almost entirely disappeared, together with the fibres of the anterior division (pars olfactoria) of the anterior commissure. The grey matter, however, remains covering the anterior and lower, and in monkeys also the upper, aspect of the tract, form-

ing the olfactory bulb. This exhibits certain peculiarities of structure, differing from the rest of the cortex (fig. 38).

The medullary fibres, in the centre of which is the remnant of the original cavity (fig. 38, 2), are covered by a layer of granules embedded in a fine plexus of nerve fibres (fig. 38, 3). This is succeeded by a layer of nerve cells resembling the pyramidal cells of the cortex, the basal processes of which are supposed to be continuous with the fibres of the tract. These cells send branching processes outwards towards the periphery (fig. 38, 4).

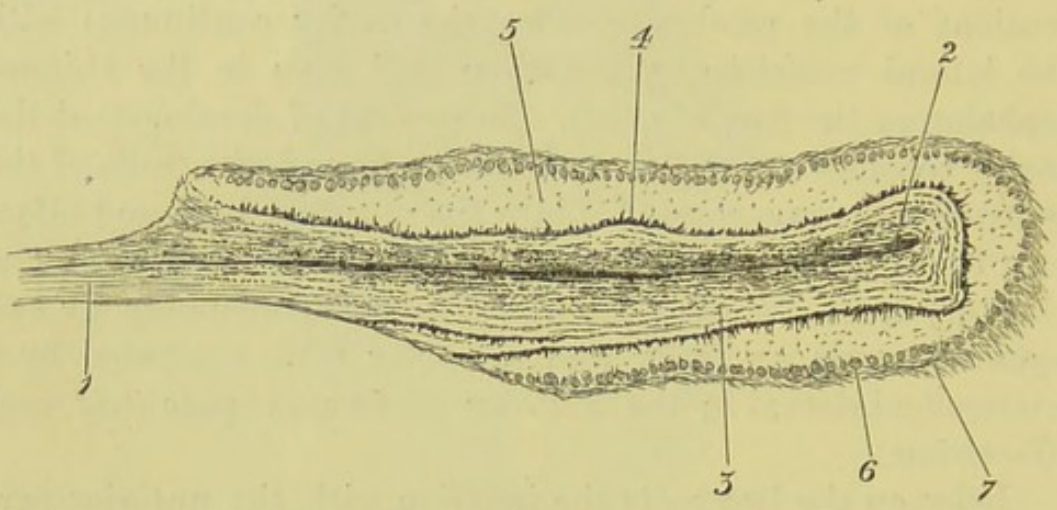


FIG. 38.—Sagittal Section of the Olfactory Bulb and Tract of the Monkey. (From a preparation and drawing by Beevor.)—1, olfactory tract. 2, central grey substance. 3, granular layer. 4, ganglionic cellular layer. 5, gelatinous layer. 6, glomerular layer. 7, olfactory nerve fibres.

The ganglionic cellular layer is succeeded by a gelatinous layer, similar to the external layer of the cortex cerebri, in which are scattered cells similar to those of the ganglionic layer (fig. 38, 5). The gelatinous layer is succeeded by a layer of peculiar roundish or oval structures termed the glomeruli olfactorii (fig. 38, 6), the exact constitution of which is not agreed on, but which are undoubtedly the primary origin of the olfactory nerves, which, collecting on the surface (fig. 38, 7) of the glomerular layer, descend through the foramina of the cribriform plate to the nasal mucous membrane.

CHAPTER II.

FUNCTIONS OF THE SPINAL CORD.

§ 1. When the spinal cord is severed transversely at any point, either experimentally or as the result of disease, all the parts below the seat of injury are paralysed, both as regards sensation and voluntary motion. But though sensation proper and volitional control are abolished, yet a number of functional manifestations of greater or less complexity are still possible both in the domain of organic and animal life—functions which are in their turn entirely annihilated when the cord itself is disorganised.

From this it is evident that the spinal cord is not merely the medium of communication between the periphery and the centres of sensation and volition, but also an independent centre, or group of centres.

We have therefore to consider the functions of the cord—first as a conductor, and second as an independent centre.

Part I.—*The Cord as a Conductor.*

§ 2. When a hemisection of the cord is made, paralysis of voluntary motion occurs on the side of lesion, and paralysis of sensation on the opposite side.

The following experiment[1] which I made on a monkey illustrates these propositions. The cord was cut on the left side, between the seventh and eighth dorsal nerves, to the extent indicated in the accompanying figure, which is after a microphotograph of the first slice from the cord above the incision. The cord, except at the region of the lesion, was otherwise intact (fig. 39).

[1] See *Brain*, April 1884, 'Hemisection of the Spinal Cord.'

Directly after this injury, and till death, eighteen days subsequently, there was, on the side of lesion, absolute paralysis of motion, and perfect retention of sensibility, not apparently heightened, to every form of stimulation, tactile and painful. The animal's attention was immediately excited by a touch anywhere on the same side below the lesion, and put its hand to, or rubbed, the part touched or pinched.

On the opposite side voluntary motion was unimpaired, and the animal was able to use its right leg freely and forcibly with perfect precision. There was, however, absolute insensibility to every form of sensory stimulation, such as contact,

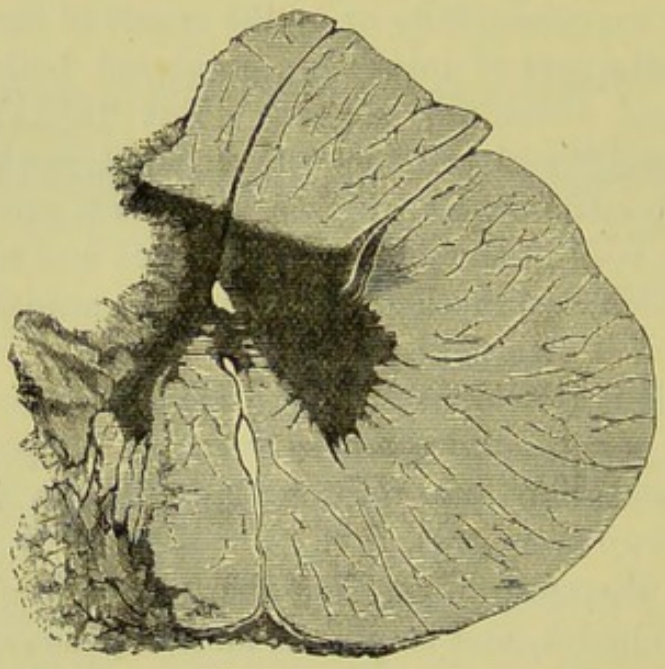


FIG. 39.—Hemisection of Spinal Cord of Monkey (microphotograph × 12). (Experiment described in text.)

pinching of the toes and muscles, and a degree of heat which excited lively manifestations of uneasiness and pain in the left leg or in the hands.

It was observed also that, though the animal could move its right leg for volitional purposes with perfect precision when the eyes were open, it could not do so when the eyes were blindfolded, being evidently unaware of the position of its leg, and unable to extricate it from any obstruction. This, however, it readily effected when the eyes were freed.

With the exception of certain statements made in reference to the muscular sense, which will be considered more at

length subsequently, the results of this experiment agree with those obtained by Brown-Séquard, and with the facts of disease or injury of one-half of the spinal cord in man. It has usually been found by other experimenters, and also in cases of unilateral disease of the cord, that on the side of lesion there is a hypersensitiveness to sensory impressions; but this was not apparent in the experiment above recorded. What the cause of this hyperæsthesia so frequently observed may be is not quite clear; but it does not appear to be an essential feature of a lesion capable of inducing total anæsthesia of the opposite side. It is probable, from the results obtained by other physiologists, that the sensory paths are not so entirely crossed in many of the lower animals as they appear to be in the monkey and man, and that the paths of voluntary motor impulse are not exclusively direct, or confined to the same side of the spinal cord.

Apart, however, from certain differences in degree, the general rule prevails, that the motor paths are on the same side, and the paths of sensation on the opposite side.

§ 3. But when we come to the exact differentiation of the sensory and motor tracts opinions become exceedingly divergent. Nor is this greatly to be wondered at. The methods of investigation so successful in determining the functions of nerves, viz. the complementary methods of excitation and section, are here most difficult of application, and the sources of error numerous. Owing to the small area in which the various tracts are compressed, it is difficult to employ electrical stimulation to excite one part without risk of extrapolar conduction, and consequent irritation of other parts. It has, indeed, been asserted by Van Deen and Schiff that, with the exception of the posterior columns, none of the rest of the spinal cord is excitable by electricity or any other form of stimulus. That this is erroneous has been satisfactorily shown by the experiments of Fick,[1] who obtained movements by electrical irritation of the anterior columns after removal of the posterior roots and posterior columns of the cord. These results have been confirmed by Mendelssohn,[2]

[1] Pflüger's *Archiv f. Physiologie*, Bd. II.

[2] Du Bois-Reymond's *Archiv f. Physiologie*, 1883, Heft 2 and 3.

who has also shown that the muscular contractions which result from irritation of the anterior columns are not reflex, as they occur sooner than when irritation is applied directly to the posterior columns, the time lost being that necessary to excite reflex action through the grey matter.

The experiments of Ludwig and Woroschiloff, mentioned below, also prove the excitability of the columns of the spinal cord. And the more recent experiments of Horsley, as well as similar facts observed by myself, show that stimulation of the lateral columns of the spinal cord induces movements in parts below the section.

But, owing to the difficulty of preventing diffusion, the method of stimulation by the electric current is liable to too many fallacies to be altogether reliable. Nor is the method of section of particular tracts free from complication, and the extent of injury really inflicted has not always been determined with that degree of accuracy necessary to ensure confidence in the results arrived at. Besides these difficulties there are others which complicate the question. In experimenting on the lower animals it is often extremely difficult, if not impossible, to discriminate between mere reflex action, which ensues on stimulation of sensory nerves, and sensation proper. The occurrence of reactions above the section, on stimulation of sensory nerves below the section, does not necessarily indicate that the paths of true sensation have not been interrupted. Such facts prove only the conveyance of afferent impressions to higher regions—a fact of great importance, but requiring interpretation in relation with the results of other methods.

§ 4. The careful and varied experiments of Ludwig and Woroschiloff[1] have shown that motor impulses may be transmitted downwards, and sensory impulses conveyed upwards, without any apparent disturbance of the normal order, when the whole of the anterior and posterior columns, and also the grey matter, have been severed, and when, therefore, only the lateral columns of the cord remain intact.

By diverse sections of one or both lateral columns, or parts

[1] *Der Verlauf der motorischen und sensiblen Bahnen durch das Lendenmark des Kaninchens*, 1874.

of them, they found that when only one lateral column remained, movements of the arms and anterior part of the body could be readily excited by irritation of the opposite leg behind the section, but only with difficulty by irritation of the leg on the same side. In order that impressions on the opposite leg should readily call forth movements in the anterior part of the body it was found, that that portion of the lateral column should remain intact, which lies in the area bounded by the prolongation outwards of the anterior and posterior commissures—the middle third. Slight movements could, however, be excited in the anterior part of the body if only the anterior or posterior third of the lateral column remained.

In respect to motor impulses their experiments showed that by sensory stimulation of parts above the lesion—the ears, &c.—movements could be excited only in the leg on the side of which at least a portion of the lateral column remained intact. If the lateral column were entirely destroyed on one side, no reflex movements whatever occurred in the leg of that side by sensory stimulation above the lesion. For the conveyance of reflex motor impulses to the leg of the same side at least the anterior half of the lateral column must remain intact. The co-ordinated movements of the leg such as are required for sitting, springing, &c. require the integrity of the middle third of the lateral column.

Electrical irritation of the cut surface of the cord, severed below the calamus scriptorius, was able to excite co-ordinated movements of the leg only on the side on which the middle third of the lateral column was uninjured. But tetanic contraction of the muscles of the other leg could also be induced, though the lateral column on this side was entirely severed.

It thus appears that the sensory impulses which excite movements in parts above the section are conveyed mainly in the opposite lateral column, and specially in the middle third of this column ; and that the centrifugal impulses which excite such movements as are characteristic of purposive co-ordination are conveyed in the lateral column of the same side, and specially in the middle third of this column. The relative facility with which sensory impressions on the leg on the side

of lesion evoke movements in the anterior part of the body is termed by Ludwig and Woroschiloff cross hyperæsthesia; and they give a hypothetical explanation of this by assuming that on the side of lesion certain inhibitory fibres have been divided. It does not appear to me that either the term or the explanation is at all necessary. The hyperæsthesia on the side of lesion is only a sign by contrast of the diminished sensibility on the other side, and as a matter of fact ceases when the other lateral column is similarly divided, and both legs are reduced to the same level of sensibility. As regards purely local reflexes, i.e. the movements of the limbs below the lesion, they found that the excitability of the limb on the side of lesion was equal to that on the opposite side to minimal stimuli; but, as the stimulation increased, the movements of the leg on the sound side became more active, unaccompanied, however, by general movements in the parts above the lesion; while the reverse was the case on the leg on the side of lesion.

While doubts may be entertained as to how far these experiments, taken by themselves, indicate the paths of sensation and volition, as distinct from mere reflexes more or less general, yet when they are viewed in connection with the results of hemisection of the cord in the monkey, and the symptoms of unilateral disease or injury of the cord in man, there seems no reason for doubt that the lateral columns contain the paths of sensation and voluntary motion; and that it is the division of these tracts mainly, if not exclusively, that causes loss of sensation on the opposite side, and loss of voluntary motion on the same side.

Ludwig and Woroschiloff have not been able to differentiate the sensory from the motor tracts of the lateral columns, and believe that they are more or less mingled together. But the facts of human and experimental pathology indicate that they are, to a large extent at least, distinctly separable from each other.

§ 5. When the motor centres of the cerebral hemispheres (Chap. X.) are destroyed, or the tracts leading from them are severed, degeneration ensues and changes occur (sclerosis) which render the position of the degenerated tracts readily distinguishable from the normal tissue.

Investigations of this nature show conclusively that when the motor centres, or voluntary motor tracts, are destroyed, degeneration proceeds downwards exclusively in the pyramidal tracts in a well-defined area of the cord.

The path of degeneration coincides exactly with the tracts, which the embryological researches of Flechsig have shown to be developed in relation with the cerebral hemispheres, and at a later period than the fundamental spinal tracts. We have thus a concurrence of experimental, pathological, and anatomical evidence determining the paths of voluntary motor impulse in the spinal cord. The pyramidal tracts, as already described, descend from the cortex through the internal capsule, foot of the crus and pons, and, decussating more or less completely at the lower anterior aspect of the medulla oblongata, proceed mainly in the opposite lateral column; while some, which do not decussate there, proceed down the anterior median column of the same side for some distance before crossing to the opposite side.

When a transverse section is made of the spinal cord itself the descending degeneration affects the same tracts, but, in addition, also certain others. These are the anterior root zones. In these, however, the degeneration proceeds downwards only a short distance; a fact which shows that the anterior root zones are not long paths of conduction from the encephalic centres, but merely centrifugal paths between higher and lower spinal segments. That they are motor is clearly shown by the direction of the degeneration, but they are motor in a different sense from the pyramidal tracts, and belong to the fundamental spinal system. As these tracts are apparently continuous with the reticular formation of the tegmentum, it would appear that the anterior root zones are the paths of conduction of motor impulses from centres distinct from those of voluntary motion proper.

The completeness of the degeneration which ensues in the pyramidal tracts when the cord is severed, or the cerebral motor centres destroyed, shows that the sensory tracts of the spinal cord, though apparently in the same region of the cord, are not confusedly mingled with those of voluntary motion. Nor when the pyramidal tracts are densely sclerosed primarily

(primary lateral sclerosis), or secondarily to cerebral lesion, is sensation impaired. It is therefore impossible to avoid the conclusion, in opposition to the hypothesis of Ludwig and Woroschiloff, that the tracts of sensation are distinctly defined and separable from those of voluntary motion.

It has not, however, been found that any tracts in the postero-lateral columns degenerate upwards when the cord is severed at any point.[1] There are certain facts which render it probable that the sensory paths lie in the lateral limiting zone[2] of Flechsig (see fig. 6) in the angle formed by the anterior and posterior horns. This region has been found quite free from degeneration when the pyramidal tracts proper have been found densely sclerosed, either as the result of degeneration secondary to cerebral lesion, or primarily in cases of lateral sclerosis with spastic paraplegia. Why, however, in this case these tracts should not degenerate upwards when they are divided is not clear, unless we assume that they maintain a continuous relation and connection with the cells of the posterior horns; and this is extremely probable.

§ 6. But while the existence of sensory paths in the lateral

[1] Gowers (*Diagnosis of Diseases of the Spinal Cord*) figures a tract (fig. 3) in the antero-lateral column of the dorsal region, which he ascribes to ascending degeneration in a case in which the lower part of the cord was crushed, and which he thinks may be the sensory path. Somewhat similar appearances, found in a case of compression of the spinal cord by a tumour, are ascribed by Westphal (*Archiv f. Psychiatrie*, Bd. x. Heft 3) to foci of multiple degeneration. Hadden has published (*Trans. Patholog. Society*, 1882) a description of a cord, in which there were symmetrical tracts of degeneration in a somewhat similar position to those of Gowers' case, in the upper cervical region and lower portion of the medulla oblongata. But there was no clinical history further than that the specimen was from that of a patient affected with locomotor ataxy. The true nature and significance of the degeneration is therefore only a matter of speculation. [Since this was in type H. Tooth (*St. Bart. Hosp. Rep.* vol. xxi.) has published a case in which there was a tract of degeneration, similar to that in Gowers' case, in the cervical region after injury of the cord in the mid-dorsal region. But as at the level of the first cervical root it merged with the direct cerebellar tract it seems probably to belong to this system.]

[2] These remain intact in a case reported by Schultze (*Archiv f. Psychiatrie*, Bd. xiv. 359, Case V.), in which, in consequence of solution of continuity of the lower cervical region, there was secondary degeneration of the pyramidal tracts, and also of the lateral columns and anterior root zones. The internal division of the lateral columns, the columns immediately in contact with the anterior horns and the limiting layer, were entirely free from degeneration.

columns is not clearly indicated by the facts of secondary degeneration, this method of research shows very conclusively that when the cord is divided ascending degeneration takes place in the direct cerebellar tracts (fig. 6, *d c*), the posterior root zones (columns of Burdach (fig. 6, *p r*), and posterior median columns (columns of Goll) (fig. 6, G).

Degeneration in the direct cerebellar tracts has been followed up to the restiform bodies and thence into the superior vermiform process of the cerebellum.

The posterior root zones degenerate upwards only for a

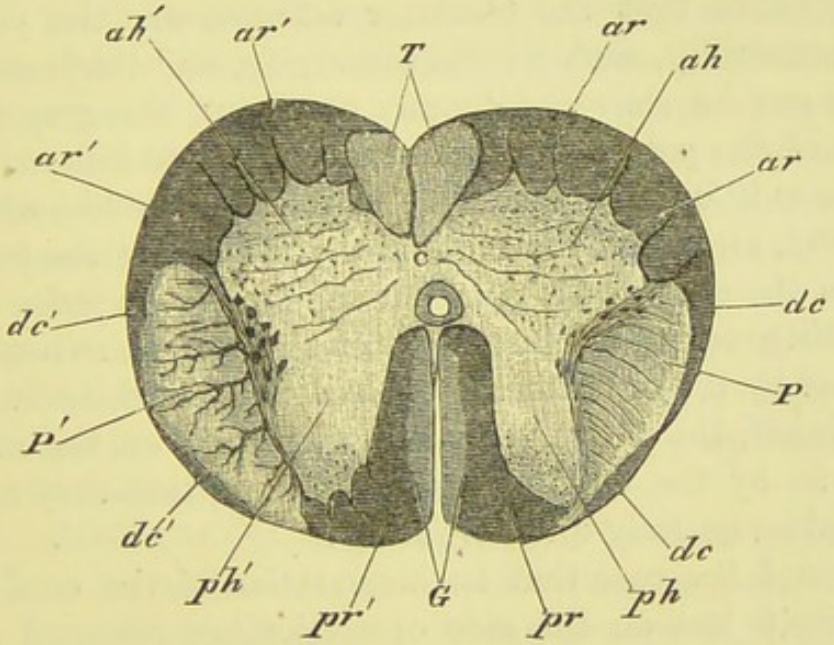


FIG. 40.—Transverse Section of Spinal Cord of Human Embryo at five months (Ross). *ah*, *ah'*, anterior horns of grey substance. *ph*, *ph'*, posterior horns. *ar*, *ar'*, anterior root zones. *pr*, *pr'*, posterior root zones. P, P', pyramidal fibres of lateral columns. T, columns of Türck. G, columns of Goll. *dc*, *dc'*, direct cerebellar tracts. *c*, anterior commissure.

short distance—at most a few segments above the lesion—while the posterior median columns degenerate, in part at least, up to the clavate nuclei of the medulla oblongata. These tracts therefore—the direct cerebellar tracts, columns of Burdach, and columns of Goll—are undoubtedly centripetal paths, whatever views may be entertained in reference to their exact functions and the nature of the impressions they convey.

The direct cerebellar tracts as described above consist of fibres which connect the cells of Clarke's vesicular column with the cerebellum, but their division does not appear to

cause any loss of sensation proper; for on the side of hemisection of the cord sensation is unimpaired, and on the side on which the tract remains sensation is entirely abolished.

What are the exact functions subserved by the direct cerebellar tracts is a matter more of speculation than demonstration, and will be discussed below in connection with the functions of the cerebellum (Chap. VI. § 24).

Respecting the posterior columns very divergent views have been entertained. At one time, from their apparent relations to the posterior roots, it was assumed as beyond all question that they were the paths of sensation. It is still held by Schiff that the posterior columns are the paths of tactile sensibility, each for the same side, and that sensations of pain can be conveyed by any portion of the grey matter. Section of the posterior columns, according to him, causes at first a condition of hyperæsthesia followed by loss of tactile sensibility, and if all the cord is divided except the posterior columns, though there is complete analgesia, the sense of contact is still preserved. These doctrines have been so completely disproved by the experiments of Brown-Séquard, Ludwig, and Woroschiloff, the above recorded experiment on the monkey, as well as by the facts of disease in man, that they must be discarded as entirely untrustworthy.

It is not the case that in hemisection of the cord tactile sensibility is lost on the side of section, or retained on the side on which the posterior column remains intact. Nor is it true that impressions of pain can still be conveyed if only a portion of the grey matter remains undivided. In the above-mentioned experiment though the whole of the grey matter of the right side was intact, as also the central grey matter and portions of the anterior and posterior horns on the left side, yet there was absolute analgesia of the right leg.

§ 7. Physiological experimenters have not distinguished between the effects of lesions of the posterior root zones (columns of Burdach) and posterior median columns (columns of Goll) respectively. They are, however, separable, and may be affected independently by diseased processes. The posterior root zones are, for a time, the paths of sensation, but this is only so until the posterior roots, which enter them

and diverge upwards and downwards, pass into the grey matter and cross to the opposite side. But the posterior median columns are the direct paths of posterior root fibres which ascend as far as the clavate nuclei of the medulla oblongata.

The posterior root zones and posterior median columns are generally affected together by primary disease, as is the case in tabes dorsalis, or locomotor ataxy, in which the lesion is a sclerosis, characterised by increase of the connective tissue and atrophy of the nerve fibres in these columns. But the columns of Burdach and columns of Goll are not always affected to the same extent, and in some cases only the columns of Burdach, and in others only the columns of Goll, have been found diseased. The characteristic symptoms of ataxy, viz. the lancinating pains and disorders of locomotion have been found by Pierret [1] and Charcot [2] to be associated with sclerosis limited to the posterior root zones. What causal relationship subsists between the symptoms of ataxy and the disease of the posterior root zones is reserved for future consideration (Chap. IV.). Here it is sufficient to remark that the ataxic symptoms are not in proportion to the extent of impairment of tactile sensibility.

The columns of Goll, as has already been stated, degenerate upwards as far as the clavate nuclei when the cord is transversely severed at any point. If the section or disease is in the dorsal region, the ascending sclerosis of the columns of Goll does not reveal itself by any symptoms in the part of the body above the lesion.

Sclerosis limited to the columns of Goll—but whether primary or secondary is not quite certain—has been observed in one or two instances. In one of these cases, reported by Pierret,[3] there were marked disorders of equilibration, and also some degree of impairment of tactile sensibility. But, as Ross [4] has remarked, the posterior root zones were also to some extent implicated in the disease. In a case related by

[1] *Archives de Physiologie*, 1872.
[2] *Leçons sur les Maladies du Système Nerveux*, tome ii. 1877.
[3] *Archives de Physiologie*, 1873.
[4] *Diseases of the Nervous System*, 2nd ed. vol. ii. p. 69.

Gowers[1] nothing was ascertained respecting the symptoms manifested during life, if any.

§ 8. It is evident from the above facts of experiment and disease that in the spinal cord there are different centripetal tracts: those of sensation proper in the lateral columns, and others, the posterior columns and direct cerebellar tracts, respecting the exact functions of which at present only theoretical speculations, in the absence of experimental demonstration, can be offered.

In regard to the paths of sensation proper it has been assumed by Brown-Séquard, on clinical grounds, that there is a differentiation of the paths for the different forms of sensibility, inasmuch as one or more may be entirely abolished while others remain intact. Thus in cases of disease of the cord pain may not be felt, while the tactile and thermal sensibility continue; and touch or tickling may be perceived, but no sense of pain can be excited by the most powerful stimulation. This hypothesis as to the existence of specific sensory paths in the cord is intimately associated with the hypothesis of the existence of specific nerves for the various forms of cutaneous sensibility. As all the facts are, in my opinion, more readily explicable on the hypothesis of differences in the peripheral organs, and in the receptivity to various forms of external agencies, of nerves endowed with common properties, so it is more probable that the common sensory paths of the spinal cord may be so affected by disease as to be unable to convey impressions of one kind, while they continue pervious to others. On what these differences may depend, however, is a question on which, in our ignorance of the molecular conditions of nerve transmission, we can scarcely ever profitably speculate at present. But such an hypothesis involves much less difficulty than that of specific nerves and sensory paths.

§ 9. It is customary to describe as a special sense the knowledge we possess of the extent and degree of our active or passive muscular movements. It is undoubtedly true, as E. Weber established, that we are able to discriminate between weights and resistances, beyond the limits of mere sensa-

[1] *Trans. Path. Soc.* 1876.

tions of cutaneous pressure, by the degree of muscular strain necessary to sustain them; and we are able to determine the position of our limbs or mobile parts, whether assumed by our own active movements or passively communicated to them.

But we have here to deal with a complex result; for, in addition to any special impressions originating in the muscles, we have impressions caused by contact and pressure, muscular displacement, tension of ligaments, and, if the weight is heavy, general bodily strain. That these enter largely into the composition of the so-called muscular sense is generally admitted, and it is absurd to describe as a special sense, with special end organs and special centripetal paths, that which is manifestly only a compound of simpler elements.

It is the rule, as laid down by Schroeder van der Kolk, that the muscles and overlying skin are innervated by the same mixed nerve; an arrangement which would account for the origin of impressions resulting from the displacement of the muscles during contraction. The joints, ligaments, and periosteum are richly supplied with sensory nerves and sensory organs—Pacinian corpuscles (Rauber), end-bulbs (Krause—which seem specially adapted to receive stimulation by mechanical pressure. In these, therefore, we have a further very evident source of impressions likely to be generated by muscular activity and movement. The muscles, also, themselves, or at least their membranous investments, have been shown by the researches more particularly of Sachs[1] and Tschiriew[2] to be furnished with a network of non-medullated nerves, derived from the posterior roots, whose course and distribution are entirely distinct from those of the motor nerves. That the muscles possess a sensibility of their own, first attributed to them by Sir Charles Bell, is proved beyond all doubt by their nervous supply and by physiological and clinical research. Though they are insensible to many forms of irritation, which act powerfully on cutaneous nerves, such as section, chemical irritation, heat and cold—facts which have led some observers to question their sensibility altogether—yet under certain conditions and modes of stimulation their

[1] Reichert and Du Bois-Reymond's *Archiv*, 1874.

[2] *Archives de Physiologie*, 1879.

sensibility becomes very apparent. They are distinctly sensible to pressure and to a painful sense of fatigue from overstraining, which is accurately localised in their own tissues. They are also the seat of painful neuroses, associated with cramp or contracture, which have been erroneously ascribed merely to pressure on transcurrent sensory nerves. That this is not the case is proved by the fact that contractions equally powerful with those seen in cramp may be induced without any such sense of pain ; and further, if the pain were due merely to pressure on transcurrent sensory nerves, it ought, according to the law of peripheral projection, to be felt, not in the region of the muscles themselves, but in the region of distribution of the nerves supposed to be compressed. The most convincing proof of the sensibility of muscles has been furnished by Duchenne, who has shown that muscles are sensible to electrical stimulation, which causes in them a certain vibratory thrill, peculiar to themselves and entirely distinct from the sensibility of the skin ; for it may be felt in muscles laid bare and denuded of their cutaneous covering.

§ 10. There is therefore ample proof of the proper sensibility of muscles, and there can be no doubt that this enters with the other factors above enumerated into the composition of the so-called muscular sense. Whether the sensibility of the muscles alone would suffice as the basis of all that is commonly included under the muscular sense is incapable of experimental determination, as section of the posterior roots of the nerves causes cutaneous as well as muscular anæsthesia.

Bernard's experiments, as well as others of a similar nature, have shown that when the posterior roots are cut, the limbs are moved with an awkwardness which is only explicable by the absence of guiding sensations, presumably muscular as well as cutaneous. There are certain clinical facts which would seem to show that the sensibility of the muscles and the muscular sense may continue though cutaneous sensibility is abolished. But, though the possibility of this cannot be denied, the actual existence of such a condition is far from being satisfactorily proved. Much of the evidence adduced is extremely unsatisfactory, and there is reason to believe that tactile sensibility is not entirely abolished, though there may

be insensibility to pain and temperature, in the cases where the muscular sense really continues. What has been commonly regarded as evidence of the existence of the muscular sense in a limb otherwise anæsthetic has no such meaning. This refers more particularly to the assertion made by Brown-Séquard, and currently accepted, that in unilateral section of the spinal cord the muscular sense continues in the limb opposite the section, notwithstanding the total anæsthesia otherwise, and is lost on the side of section. The existence of the muscular sense is inferred merely from the fact that the limb can be moved freely and forcibly and directed without uncertainty, for volitional purposes even when the eyes are shut. But that this is possible in the entire absence of any sense of movement has been conclusively demonstrated by a case of spinal disease reported by Schüppel [1] in which motor force, and the power of directing the limb for volitional purposes, were shown to exist though the limbs were otherwise entirely devoid of sensibility, cutaneous as well as muscular. In the experiment on the monkey above recorded it was found that, though movements could be intended and carried out in the absence of hindrance, yet when the eyes were blindfolded the animal seemed utterly ignorant of the position of its leg, and unable to extricate it from an obstacle interposed against its intended movement. And that the muscular sense is not lost on the side of section has been shown by Köbner,[2] who on applying proper tests to the paralysed limb, in a case of unilateral disease of the cord, found that the patient had a perfect knowledge of every movement passively communicated to it.

There does not appear to be a single fact which would indicate that the muscular sense can be abolished, and the other forms of sensibility of the limb continue.

Even if it were the fact that muscular sensibility might continue in a limb otherwise insensible, in cases of spinal disease, it would by no means follow that the paths of muscular sensibility were anatomically separable from those of common sensibility. The same hypothesis is applicable

[1] *Archiv d. Heilkunde*, 1874, vol. xv. p. 44.

[2] *Deutsch. Archiv f. klin. Med.* 1877, Bd. xix. p. 169.

here as that advanced to account for the abolition of one form of sensibility and retention of others.

Under no circumstances whatever can Brown-Séquard's doctrine be accepted, that the paths of the muscular sense are in the anterior roots and motor tracts of the spinal cord. This is so utterly opposed to every well-established fact respecting the anatomy, physiology, and pathology of the anterior roots that it seems a marvel that such a doctrine should still be mentioned otherwise than to be condemned.

The anterior roots have a distribution in muscles entirely distinct from the sensory roots; irritation causes muscular contraction only, and in those cases where muscular sensibility has been entirely abolished—as in Schüppel's case above mentioned—the anterior roots have been found in a perfectly normal condition. On the other hand, as I have elsewhere shown,[1] in cases of anterior polio-myelitis, where the anterior roots and muscular fibre have entirely disappeared, the so-called muscular sense continues unimpaired, and the patient is able, blindfold, to state accurately the position and degree of strain which are passively communicated to his paralysed limb.

It is abundantly evident from facts such as these that the sensations arising in connection with muscular action are of a purely centripetal character, and are conveyed by the posterior roots and sensory tracts of the spinal cord along with the other forms of common and tactile sensibility.

Part II.—*The Spinal Cord as an Independent Centre.*

§ 11. The spinal cord possesses functions as an independent centre, a knowledge of which is necessary for the exposition and comprehension of the functions of the brain proper. The functions of the cord as a centre are of the same kind as those which we observe in their greatest simplicity in the nervous mechanism of many of the invertebrata. In the ascidians, the ancestral type of the vertebrates, the nervous apparatus consists of a central ganglion (fig. 41, *c*) connected with the periphery by two sets of nerve filaments. One set

[1] *Brain*, April 1884.

is distributed to a part of the integumentary surface, capable of receiving and being acted on by external stimuli (*a*); the

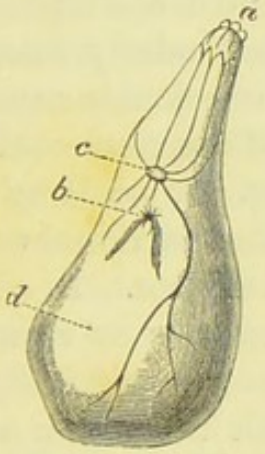


FIG. 41.—Nervous System of an Ascidian (Carpenter.)—*a*, the mouth. *b*, the vent. *c*, the ganlion. *d*, the muscular sac.

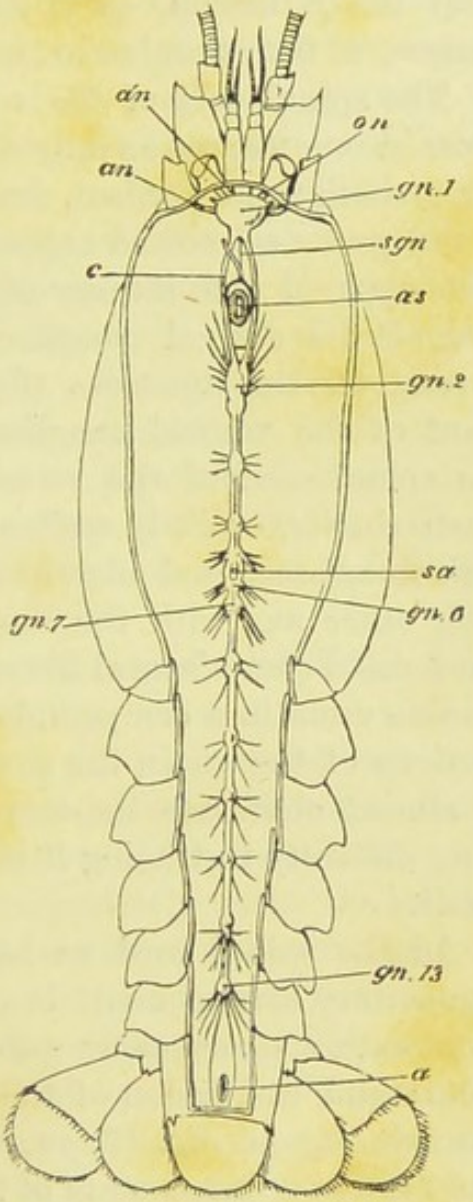


FIG. 42.—Nervous System of the Cray-Fish (Astacus fluviatilis). (Huxley.)—*a*, vent. *an*, antennary nerve. *a'n*, antennulary nerve. *c*, circum-œsophageal commissures. *gn.* 1, supra-œsophageal ganglion. *gn.* 2, infra-œsophageal ganglion. *gn.* 6, fifth thoracic ganglion. *gn.* 7, last thoracic ganglion. *gn.* 13, last abdominal ganglion. *œs*, œsophagus in cross section. *on*, optic nerve. *sa*, sternal artery in cross section. *sgn*, stomatogastric nerve.

other is distributed to muscular fibres, which on contraction cause diminution of the body cavity (*d*).

Impressions made on the sensory surface are conveyed by the afferent fibres to the central ganglion, whence an impulse

is conveyed by the efferent fibres, causing contraction of the muscular fibres. This is a type of what is termed *reflex action*, from the reflection, as it were, through the energy of the centres, of the stimulus to the periphery.

The spinal cord of the vertebrate animals may be looked upon in one respect as only a more complex form of an essentially similar mechanism, and may be regarded as composed of thirty-one connected segments, more or less fused together, each segment with its pair of nerves being a bilateral repetition of the central ganglion with its afferent and efferent fibres. In the annulosa (fig. 42) the segmentary arrangement of the ventral ganglionic chain, which corresponds to the spinal cord of the vertebrates, is particularly manifest. Each somite, or body segment, has its own double ganglion, with its afferent and efferent fibres, but all are connected with each other and with the head centre (fig. 42, *gn.* 1) by what are termed commissural fibres, whereby the individual centres become units in a compound or collective system. In certain portions of the chain the ganglia fuse together so closely as to almost obliterate the segmentary arrangement; but there is no difficulty in tracing it in relation with the fusion of the somites.

In the spinal cord, as has been stated above (p. 7), the segmentary arrangement is evident in the larger amount of grey matter corresponding to the attachment of the anterior roots; and the fusion of the ganglia of the cray-fish in the thoracic region (fig. 42, *gn.* 6) has its analogy in the cervical and lumbar enlargements of the cord in vertebrate animals.

§ 12. The spinal cord as a whole, and its individual segments, are capable of independent activity, similar to that of the ascidian nervous mechanism, when the cord is separated from the higher centres, or the segments from each other.

If the body of a frog be divided transversely the lower half will still retain its vitality for a considerable period. If the foot be irritated the muscles of the leg will be thrown into action, and this will occur so long as the grey matter of the cord is intact, and its connections with the periphery are maintained.

After section of the cord in warm-blooded animals the

same reflex contraction of the muscles is caused when a part is irritated below the line of section.

A similar experiment is frequently performed by injury or disease in man. Where as the result of injury or disease there is a solution of continuity of the cord at any point, all the parts deriving their nervous supply from the cord below the seat of lesion become paralysed as regards sensation and voluntary motion. But if the soles of the feet are tickled the legs will be thrown into active movements, of which the individual is not conscious, and which it is out of his power in the slightest degree to control. These are examples of reflex action, and the phenomena observed in man are of especial importance in reference to the interpretation of similar phenomena in the lower animals, since in man we are able to ascertain without doubt that consciousness is not necessarily a concomitant of reflex action.

When the brain and cord are connected, and if the brain is in a state of wakeful activity, the same stimulus which gives rise to reflex muscular action will also excite sensation, but the perception of the impression is no essential factor in the process. If the sole of the foot of a person asleep be tickled the leg will be withdrawn, precisely as in the waking condition, and with the same appearance of purposive adaptation, but without consciousness on the part of the individual.

Though the phenomena of reflex action are manifested by the spinal cord and its segments when completely separated from the brain, yet under normal conditions they are not dissociated, and it is therefore not likely that the laws and conditions of reflex action are the same under both circumstances. When the spinal centres form only a part of the whole cerebro-spinal system, stimuli which excite reflex action also affect the whole nervous system, cerebral as well as spinal. And certain facts of experiment, as well as of clinical observation, tend to show that even in what looks like simple spinal reflex action the cerebral centres form an important factor, as indicated by the differences observable in the reflex actions of the two sides, when lesion exists in one hemisphere (see p. 375).

§ 13. But it would appear that when the spinal centres are completely dissevered from the cerebral, their activity is

more readily excitable than under normal conditions. Ward[1] has shown that when the supra-œsophageal ganglion, or brain of the cray-fish (fig. 42, *gn.* 1), is detached from the rest of the cord the lower centres exhibit an almost incessant aimless activity. In the absence of the brain, therefore, the lower ganglionic centres would seem to be more readily dischargeable; or, expressed in another way, the brain seems to inhibit the tendency to wasteful activity on the part of the lower centres. The same thing has been demonstrated in the frog in the following manner. A frog is suspended by the head, and the legs, which hang down, are allowed to dip into a vessel containing dilute acid. After a certain interval the irritation of the acid causes the legs to be withdrawn. The average interval is determined by repeated trials. The cord is then cut below the medulla oblongata and the experiment repeated. The interval which now elapses, between contact with the acid and the withdrawal of the feet, is considerably shortened, and the action is also observed to be more energetic.

In man also, when, in consequence of disease, the continuity of the cord is completely interrupted at any point, the reflex excitability of all the parts below the injury is in a similar manner greatly increased.

It is not, however, necessary to assume, as Setschenow[2] and others have done, that there is anything specific in this apparent restraining or inhibitory action of the encephalic centres, or that there are special inhibitory centres in the brain. Setschenow ascribes inhibitory functions to the optic thalami and optic lobes in frogs on the following grounds. When a frog is suspended in the manner indicated above, and the average time of reflex reaction determined, it is found that the application of an irritant, *e.g.* common salt, to the optic lobes causes the interval between the cutaneous stimulation and the withdrawal of the foot to be greatly prolonged. Most people can, by an effort of will, restrain, if not altogether prevent, the reflex movements of the leg, which otherwise occur in such a lively manner from tickling the sole of the foot.

[1] 'Observations on the Physiology of the Nervous System of the Cray-fish,' *Proc. Roy. Soc.* vol. xxviii. p. 379.

[2] *Phys. Stud. ü. d. Hemmungsmechanismen*, 1863.

But neither Setschenow's experiment, nor this apparent volitional inhibition of reflex action demands any specific mechanism, apart from those concerned in the usual sensory and motor functions of the organism.

The increase of reflex excitability in the cord as a whole, after removal of the cerebral hemispheres, is true also of each segment of the spinal cord isolated from the rest. Thus Schiff[1] has shown that the reflex movements of the tail of a decapitated lizard increase in vigour with successive removal of the spinal segments from above down to that with which the afferent and efferent nerves of the tail are in relation. It is probable, therefore, that the more the afferent impulse is restricted to the centre on which it primarily impinges, and the less the diffusion into other tracts and centres, the greater is the reflex discharge. We have therefore as much ground for saying that each higher segment of the spinal cord inhibits the lower as that the brain inhibits the cord as a whole.

Setschenow's experiment and volitional inhibition appear to be only individual examples of the general law that reflex action is liable to be arrested, or interfered with, when the centres engaged in it are solicited at the same time from other quarters. Thus if, when a reflex action is initiated, a sensory nerve in some other part of the body is irritated, the reflex action is at once arrested. This has been shown very clearly by Goltz and Freusberg,[2] Schiff, and many other experimenters.

Though we may not be able to explain the exact mode in which nervous impulses interfere with each other, yet that this inhibition is a mere question of interference does not seem doubtful. Similar in action to a peripheral sensory stimulus is irritation of sensory tracts, or the excitation of sensory centres. Reflex action may be inhibited by an emotion, of which the instances are so numerous that they will occur to anyone.

Setschenow's experiment is in all probability merely the influence of irritation of sensory centres and tracts, which are undoubtedly present in the optic thalami and optic lobes.

[1] *Lehrbuch der Physiologie*, p. 200.

[2] 'Die Functionen des Lendenmarks des Hundes,' Pflüger's *Archiv*, Bd. viii. p. 460.

During volitional inhibition we are conscious of exertion in some direction. Most commonly we throw the muscles, which we wish to restrain from reflex action, into a state of tension. But in this way we are merely acting on the same centres, and thereby interfering with the reflex discharge which would otherwise take place. We can only volitionally interfere with reflex action when the efferent mechanism is subject to volitional impulse. We have no power, therefore, over the reflex actions of the organic muscles, directly at least.

§ 14. The extent and character of the reflex movements vary with the degree and locality of the stimulation. As a rule, a moderate stimulus excites reflex action in the muscles of the region anatomically in closest relation with the sensory nerves irritated.

Tickling the sole of the foot gently causes reflex withdrawal of the foot alone. If, however, the stimulation is more intense the area of reflex action becomes more extended. The muscular contractions are no longer confined to one group or one limb, but may occur on both sides and in all four limbs.

When bilateral reflex action is excited by unilateral stimulation the action is, according to Pflüger, symmetrical, i.e. the corresponding muscles are excited on both sides; but Luchsinger[1] has shown that in quadrupeds diagonal reflexes occur. Thus the one fore limb and the opposite hind limb are excited together, corresponding to the functional association of the limbs in the ordinary mode of progression.

A general excitation of all the spinal centres may occur from excessive irritation at any one point, and a similar result follows if, in place of the irritant being intensified, the excitability of the cord is heightened. Thus in certain forms of disease, and as the result of certain poisons, notably strychnia, the excitability of the cord is so increased, and the resistance to radiation so diminished, that a degree of irritation which normally would excite limited muscular action is sufficient to induce reflex spasm of all the muscles of the trunk and limbs.

§ 15. The reflex movements of the spinal cord are not mere muscular contractions of an indefinite or aimless character, but possess the distinctive features of adaptation; and this

[1] Pflüger's *Archiv*, Bd. xxii.

to such an extent as to have given rise to considerable discussion as to whether or not they imply sensation and volition on the part of the spinal centres.

They are movements either of defence or preservation, and are in general adapted either to withdraw the part from the source of irritation or to repel the irritant itself. Thus the extended leg becomes flexed or withdrawn when the toe is pinched, and if the irritant be applied to the anal region, adapted movements of both legs are made with a view to remove it. And many other co-ordinate adapted movements might be instanced.

Sometimes there is an appearance of deliberation and choice, as illustrated by the well-known experiments of Pflüger,[1] and similar ones by Auerbach, Lewes, and others.

When a drop of acetic acid is placed on the inner side of the thigh of a decapitated frog, the foot of the same side is raised and attempts are made to rub the part. On the foot being amputated, and the acid applied as before, the animal makes a similar attempt, but failing to reach the point of irritation with the stump, after a few moments of apparent indecision or deliberation, raises the other foot, and with this attempts to rub the seat of irritation.

This experiment proves at least that what is termed reflex action is not a rigidly invariable movement like that of the wheels and levers of a machine, which will only go faster or slower according to the strength of the motor, but never vary its character ; but rather a mode of reaction which varies with the intensity of the stimulation and the vital conditions of the organism. G. H. Lewes,[2] however, sees in this selective adaptation, or power of fluctuating combination in accordance with external conditions, proof of sensibility or sentience ; and he assumes that the activity of the spinal cord, as of all nerve centres, implies feeling or sensation. But if we regard mere adaptation in accordance with external conditions as indicating sensation and volition, we should be logically bound to attribute the same to plants, in which this adaptation is often remarkably conspicuous.

[1] *Die Sensorischen Functionen des Rückenmarks*, 1853.

[2] *The Physical Basis of Mind*, 1877.

It is certain that the reactions of the spinal cord severed from the brain do not affect the consciousness of the individual. But this, according to Lewes, does not disprove the existence of consciousness in the spinal cord, which may be inferred from the character of its reactions.

The question turns mainly on the use of terms. Though we may admit that the activity of all nerve centres, cerebral as well as spinal, is fundamentally of the same order, it involves large assumptions, and introduces much confusion into our language, to speak of the reactions of the spinal cord in terms which indissolubly connote states of consciousness in the individual. It seems in every way preferable to extend the range of reflex action to the brain, than to apply to the spinal cord terms which imply subjectivity, the existence of which can be proved only in connection with the activity of the cerebral centres.

But it seems to me that the appearance of deliberation and power of fluctuating combination seen in Pflüger's experiment has been greatly over-estimated. Though the irritation caused by a drop of acid usually at first causes movements only of the same limb, I have not unfrequently, in repeating the experiment, observed both feet simultaneously brought up to the part, with a view to repel the cause of offence. In this we have an instance, among many others, of the association in the cord of the centres of movements of the same kind in both limbs, due either to commissural connections or to physiological association in past experience, or both together.

Such being the case, it is not difficult to conceive that, when the relief offered by scratching at or near the part is not attained when the foot is amputated, the continuance of the irritation brings the other leg into play by associated reflex action. It is not even necessary to amputate the foot, for, after repeated stimulation of the same point, the leg of the same side becomes exhausted, whereupon the other foot is brought up to the part on each re-application of the irritant.

§ 16. That the spinal cord has no feeling in the ordinary sense of the term is shown by one among many other ingenious experiments made by Goltz.[1] He took two frogs, one

[1] *Beiträge zur Lehre v. d. Functionen d. Nervencentren d. Frosches*, 1869.

of which was decapitated, the other intact, except that it was blinded in order to prevent the occurrence of voluntary movements consequent on visual sensation. Both were placed in a vessel of water, and the temperature gradually raised. Both remained still till the temperature reached 25° C. The frog with brain uninjured began to manifest signs of discomfort followed by attempts to escape as the temperature rose, until finally it died of tetanic heat-rigidity at a temperature of 42° C. All this while the brainless frog remained perfectly still.[1] But —and it is worthy of note—while sitting in the hot water, it made the usual reflex defensive movements when acetic acid was applied to the skin. Beyond this it remained perfectly quiet, and died of heat-rigidity at 50° C.

This experiment proves in the most conclusive manner that a stimulus which, under ordinary circumstances, causes the most manifest signs of pain, causes no such manifestations in the absence of the brain. It also shows that it is not any and every kind of stimulus which is adapted to call forth reflex reaction. This occurs most readily in response to a sudden stimulus. The gradual rise in temperature increased the signs of pain in the normal frog, but failed to excite reaction in the brainless one, though the mechanism was still responsive,[2] as shown by the results which followed the application of the acid.

§ 17. It is clear, from an examination of the reactions of the brainless frog, that the movements are not mere muscular

[1] Steiner, however (*Physiologie des Froschhirns*, 1885, p. 70), says that this is not strictly true; and that, even under such circumstances, raising the temperature causes distinct movements.

[2] M. Foster ('The Effects of a Rise in Temperature on Reflex Actions in the Frog,' *Journal of Anatomy and Physiology*, vol. viii. 1874) shows that heat has a depressing or paralysing effect on the spinal centres. But the absence of reaction in the decapitated frog to a temperature which is exciting the most violent signs of sensation in the normal one, is clearly not due to paralysis of the spinal centres or reflex mechanism, inasmuch as at this time reflex action is manifested as usual to appropriate stimuli.

G. H. Lewes, in a review of the first edition of this work (*Nature*, Nov. 23, 1876), seemed to think that Foster's results required a different view to be taken of the facts of Goltz's experiment. The essential point of this, however—viz. the absence of reaction to a temperature evidently painful to a normal frog, and the continuance of responsiveness to appropriate stimuli of reflex action—remains entirely independent of the question as to the exact mode of explanation.

contractions of individual muscles, but muscular combinations of greater or less complexity acting synergically for a definite end. It is obvious, therefore, that the spinal centres are themselves the co-ordinating centres of a great variety of adapted movements.

The facts of pathology[1] show that in cases of disease limited to certain regions of the anterior horns of the spinal cord (*poliomyelitis anterior*) certain synergic combinations of muscles become paralysed, altogether irrespective of their anatomical nervous supply.

And my colleague Professor G. F. Yeo and myself have shown[2] that the stimulation of each motor root of the nerve plexuses of the limbs in monkeys, calls forth combined movements involving the co-operation of numerous muscles, widely separated from each other anatomically, but all resulting in actions such as are seen to be constantly associated together in the ordinary modes of activity of the animal.

Thus stimulation of the second dorsal root excites the action of the intrinsic muscles of the hand, as seen when the animal is resting on a perch; the first dorsal brings into play a great number of muscles, the general result of which may be compared to plucking a fruit and drawing it towards the trunk; the eighth cervical causes a combination of movements which bring the tips of the fingers into the position requisite for scratching the buttocks—the *scalptor ani* action; the seventh cervical innervates the muscular actions which, supposing the hands were the fixed point, would cause the body to be raised up, as in mounting a branch or trapeze; while the sixth cervical brings the hand up to the mouth. Stimulation of the fifth cervical causes the arm and hand to be raised upwards and backwards.

Of the roots forming the crural plexus, the fourth lumbar (third in man) innervates the flexion of the thigh on the pelvis and extends the leg; the fifth (fourth in man) extends the

[1] E. Remak, 'Die Localisation atrophischer Spinallähmungen,' *Archiv für Psychiatrie*, 1879. Ferrier, 'The Localisation of Atrophic Paralyses,' *Brain*, vol. iv. 1881-82.

[2] 'The Functional Relations of the Motor Roots of the Brachial and Lumbo-Sacral Plexuses,' *Proceedings of the Royal Society*, No. 212, 1881. See also *Proc. Roy. Soc.*, No. 225, 1883.

thigh and leg, and depresses the great toe—the propulsive action of the leg preparatory to the swing forward in walking; the sixth (fifth in man) excites a complex assemblage of movements seen in the monkey when it scratches its abdomen with its toes; the seventh (first sacral in man) causes flexion of the leg and toes similar to the action of the eighth cervical in the upper extremity; while the first sacral (second sacral in man) innervates the intrinsic muscles of the foot.

The mode of distribution of the motor roots of the plexuses of the limbs, and the functional combination which each presides over, will be found in all probability to differ in every order of animals in accordance with their ordinary modes of activity. So far as this question has been investigated, such seems to be the case. Similar experiments by Bert and Marcacci [1] on the roots of the crural plexus in the dog indicate very different actions from those observed in monkeys.

These facts render it probable that each segment of the cervical and lumbar enlargements of the spinal cord, whence nerves proceed to the limbs, is a centre of co-ordinated synergic muscular movements, of a character adapted to the habits and requirements of the animal in its ordinary modes of activity.[2]

[1] *Bull. Soc. de Biologie*, July 1881.

[2] That the motor nuclei of the various muscles represented in each root are anatomically localised in each segment is most probable, both from a consideration of the facts of disease (see *Local. of Atrophic Paralyses, supra cit.*) and from the results of direct excitation of the segment.

I am aware of the numerous sources of fallacy in applying electrical stimulation to the spinal cord, but I have on two occasions obtained results in monkeys which speak in favour of the direct excitability of the anterior horns. The spinal cord was cut above the sixth cervical root, and the cord stimulated with a weak faradic current in the following manner. A flat electrode with a superficies of six square inches was applied over the sacrum as a neutral point, and a slightly blunted needle used as the exciting electrode. On the application of the needle—under magnifying power—to the anterior horn the same action was produced as by direct stimulation of the sixth anterior root. No such effect followed the application of the needle to any other part of the cut surface, even though actually nearer the point of attachment of the root in question.

It may be said that, granting there was no conduction of currents, yet the effect depended on the irritation of the axis cylinders of the anterior roots radiating in the grey matter. This may be; but the axis cylinders being mere prolongations of the multipolar cells, probably the cells themselves are also directly excitable.

§ 18. The experiments of Ward,[1] and also those of Yung,[2] show that in the cray-fish each segment of the ganglionated cord is the centre for the movements of the corresponding somite. That the same holds good of the segments of the cord in vertebrates, though perhaps not to the same degree of independence seen in the cray-fish and other members of the annulosa, is proved by the experimental determination of the position of other centres for actions of a considerable degree of complexity. After section of the spinal cord above the lumbar enlargement in dogs, Goltz and Freusberg[3] have found that erection can be readily induced by gentle stimulation of the sensory nerves of the penis and neighbourhood. Generally associated with this also are extensor movements of the hind legs. Seminal ejaculation may also occur, according to the observations of Brachet. In female dogs, similarly operated on, impregnation may be effected; and at the full time the expulsive mechanism of parturition comes into operation in a perfectly normal manner, independently of any conscious or volitional efforts.

The bladder also empties itself on stimulation of the pelvic or anal region, or by raising the animal on its hind legs when the bladder is full. The sphincter ani is maintained in a state of activity, and contracts reflexly on gentle stimulation or the introduction of a finger within it. Goltz finds in the latter case that the contraction of the sphincter occurs with rhythmical pauses; and Freusberg observed also peristaltic action of the rectum sufficient to expel a thermometer introduced within it.

The manifestation of any of these reflex acts in response to their appropriate stimuli is at once checked by the simultaneous irritation of a sensory nerve in some other part of the body.

The experiments of Birge also (Du Bois-Reymond's *Archiv*, 1882, Heft 5 and 6) show that mechanical stimulation of the anterior horns by a needle-point produces effects which are probably due to excitation of the grey matter itself.

[1] *Supra cit.*

[2] 'Sur les Fonctions de la Chaîne Ganglionnaire chez les Crustacés Décapodes,' *Comptes Rendus*, lxxxviii. 1879.

[3] 'Ueber die Functionen des Lendenmarks des Hundes,' Pflüger's *Archiv für Physiologie*, Bd. viii. 1874.

The centres for these various acts lie in the lumbar region of the cord, and they all cease on destruction of this region. The special centre of each has been further defined in dogs and rabbits by the experiments of Budge, Gianuzzi and Masius, Körner, and others. In man we may assume from anatomical data that they are situated in the lower portion of the lumbar enlargement, in the segments related to the motor nerves below the second sacral.

The segments of the dorsal region of the cord, besides such relations as they may have with the viscera through the sympathetic system, are evidently in relation with the thoracic muscles. As these play an important part in respiration it would seem *a priori* possible for the dorsal centres to act reflexly as more or less independent respiratory centres. Langendorff[1] has actually found that when the cord is divided below the calamus scriptorius, and therefore below the respiratory centre *par excellence* (see Chap. III. § 6), respiratory movements may still be elicited for a short period at least by stimulation of various sensory nerves.

§ 19. A centre is usually described as existing in the lower cervical and upper dorsal region of the spinal cord, from which originate the fibres of the cervical sympathetic, which cause dilatation of the pupil—the *cilio-spinal* centre (Budge and Waller). Certain experiments which I have made on monkeys in reference to this point[2] have shown, with great definiteness, that there is only one spinal nerve which has this effect, viz. the second dorsal. Stimulation of the anterior root of the second dorsal, after division of the posterior root, causes dilatation of the pupil on the same side. Stimulation of the dorsal roots below this as far as the eighth, and of the first dorsal and lower cervical, causes no such action. It is possible that the position of the dilator fibres may be different in other animals,[3] but there is every reason for regarding the results obtained in monkeys as directly applying to man.

[1] *Archiv für Anat. u. Physiologie*, 1880.

[2] *Proceedings of the Royal Society*, No. 225, 1883.

[3] Gaskell (*Journ. of Physiol.*, vol. vii.) finds that in the dog the second thoracic especially dilates the pupil, and in the frog the anterior root of the fourth nerve.

There may also be other dilating fibres of the iris besides those of the second dorsal. Bulogh[1] holds that dilator fibres of the iris spring from a centre in the medulla oblongata, probably coinciding with the origin of the trigeminus, and proceed to the iris in the first or ophthalmic division of this nerve.

But whether this be so or not, there is the best evidence that the pupil can be made to dilate by irritation of the cephalic end of the divided cervical sympathetic, and these fibres are derived in the monkey from the second dorsal nerve.

But it does not follow that the centre which presides over the dilatation of the pupil is itself situated in the upper dorsal region of the cord, for the nerves which pass out by the second dorsal may have their origin higher up; and that such is the case is on other grounds highly probable (see further on this subject, Chap. III. p. 102, note).

§ 20. These various centres in the spinal cord are, though to a considerable extent autonomous, connected together and with higher centres by the associating and longitudinal tracts of the spinal cord. But all influences proceeding from the cerebral centres must act through the primary co-ordinating spinal centres. In regard to the volitional movements of the limbs there is evidently a further differentiation of the motor combinations than exists in the spinal segments, but we cannot volitionally isolate the action of any muscle from those which are physiologically synergic with it. We cannot powerfully innervate the flexors of the fingers without at the same time innervating the extensors of the wrist and fingers, nor flex a single finger without also innervating its extensor. This synergy is, as we have seen, provided for in the spinal centres of the limbs. But if this is so, it becomes improper to speak of the existence of paths of motor co-ordination in the spinal cord. The mechanism of motor co-ordination already exists. The paths are merely centrifugal tracts which call them into action. The centres of the movements of the limbs and those of the skeletal muscles are under volitional control, but those of the viscera and their outlets are less obviously so, though undoubtedly influenced by ideational and emotional states.

[1] Quoted in Hermann's *Physiologie*, vol. ii. Part I. p. 249.

The mode of action of the cerebrum on the centres regulating the evacuations is obscure. In the case of the vesical centre, however, Mosso and Pellacani[1] have arrived at the conclusion that volitional impulses acting directly on the detrusor urinæ, without the aid of the abdominal muscles, pass down the cord, probably in the posterior part of the lateral columns, and that the mechanism of evacuation simply depends on the contraction of the detrusor overcoming that of the sphincter.

§ 21. The grey columns of the cord, besides containing in their several segments differentiated centres for combined muscular actions, called into play intermittently, in connection with volitional movements of the limbs, or with the expulsion of the contents of the genito-urinary and alimentary viscera, also exercise an important influence, in many respects still very obscure, on the tone of muscles and the walls of blood-vessels, the secretions of the skin, production of heat, and nutrition of the tissues. This influence is more or less continuous, to some extent, perhaps, automatic and subject to rhythmical variations, but is in great measure dependent on centripetal influences conveyed from the periphery by the posterior roots.

Muscles are usually in a state of tension, so that when cut their ends retract. This is in virtue of their elasticity. But in addition to this they possess a certain degree of *tone*, or semi-contracture, which ceases on destruction of the spinal segment, or the afferent and efferent fibres, with which the muscles are connected. Some physiologists have questioned the existence of a muscle tone, and mainly on the ground that a muscle does not elongate when its nerve is cut. But the experiments of Brondgeest[2] have shown that the muscles of the limbs, and sphincters, become flaccid on section of the posterior roots of the nerves supplying them; and Steinmann and Cyon[3] have proved by exact measurements that the gastrocnemius of the frog lengthens appreciably on section of the posterior roots. Tschiriew[4] has demonstrated the same length-

[1] 'Sur les Fonctions de la Vessie,' *Archives Italiennes de Biologie*, tome i. 1882.

[2] *Archiv für Anat. u. Physiologie*, 1860.

[3] *Archiv für Physiologie*, 1874, p. 347.

[4] 'Tonus quergestreifter Muskeln,' *Archiv f. Anat. u. Physiol.*, 1879, p. 78.

ening in the extensor cruris of the rabbit after section of the anterior crural nerve.

The negative results of previous experiments must, therefore, be attributed to faulty methods, and the existence of a muscular tone, of a reflex character at least, must be considered as proved.

Intimately related to this muscular tone is a phenomenon which in its modifications is of great significance in the diagnosis of disease. When the ligamentum patellæ of the dependent leg is smartly struck, the point of the toe is almost immediately thrust outwards, owing to contraction of the extensor muscle of the leg. This has been termed the patellar tendon-reflex, knee-jerk, and other names.

It is not confined to the tendon of the quadriceps, but is better seen here than elsewhere under ordinary conditions. It is rarely absent in health, but in certain diseased conditions, particularly tabes dorsalis, or locomotor ataxy, and atrophic paralysis, it is entirely abolished, while it is increased in cases of disease (sclerosis) of the lateral columns, and under certain functional conditions apart from organic lesion.

As the integrity of the reflex arc—i.e. afferent nerve, centre and efferent nerve—is necessary to the existence of the 'tendon reflex,' it was regarded by Erb,[1] who first described the phenomenon, and Tschiriew[2] who first investigated it experimentally, as a true reflex similar to the cutaneous reflexes. But Westphal[3] looked upon it, more correctly, as a direct muscular contraction induced by the sudden tension which is caused by the blow on the tendon. It may in fact be regarded as a method of demonstrating the existence of muscular tone, of which it is merely an expression.

That it is not a reflex contraction is conclusively demonstrated by the measurement of the time that elapses between the percussion and the contraction. This, according to the measurements of Tschiriew (·033 sec.), Brissaud[4] (·035—·05 sec.), and Waller (·035—·04 sec.), is much more rapid than the most rapid reflex action. And Waller[5] has also shown that

[1] *Archiv für Psychiatrie*, Bd. v. 1875. [2] *Ibid.* Bd. viii. [3] *Ibid.* Bd. v.
[4] *Contraction Permanente des Hémiplégiques*, 1880.
[5] 'On Muscular Spasms known as "Tendon Reflex,"' *Brain*, vol. iii. 1880.

the time is the same for all muscles; that there is no relation between the time and the length of nerve to be traversed; and that the percussion interval is precisely the same as that of the direct mechanical excitation of a muscle.[1]

But though we cannot regard the tendon reaction as a true reflex, we may take it as an indication of the existence of muscular tone, which depends essentially on reflex influences and is of the utmost importance in the co-ordination of movements (see Chap. IV. § 18).

§ 22. The tone of the blood-vessels is also largely dependent on the spinal centres. Though the chief centre of vascular innervation is in the medulla oblongata (see below, Chap. III. § 8), and therefore general vascular dilatation follows section of the cord below the calamus scriptorius, yet this is not altogether permanent, and a further dilatation occurs on destruction of the spinal centres.[2]

The functional activity of the various tissues and organs must necessarily be associated with increased vascularity, if vitality and repair are to continue. Hence the condition of the blood-vessels, whether they are in a state of spasm or paralysis, must lead to important modifications of the nutrition and vital activity of the tissues. There has been a general tendency to ascribe all such modifications of nutrition, secretion, and the like, to variations of vasomotor innervation primarily, and to the tissues only indirectly.

But the researches of Bernard, Heidenhain, &c. on the physiology of secretion show that the nervous system has a direct influence on secretory structures independently of the vascular system.

This was first demonstrated in the case of the submaxillary gland. It is found that stimulation of the chorda tympani

[1] Among other arguments which may be adduced against the reflex nature of the so-called 'tendon reflex' is the fact that it does not follow the variations of the true reflexes. In a curious case which I reported ('Case of Allochiria,' *Brain*, Part XIX. 1882), in which there was transposition both of sensory localisation and of the cutaneous reflexes, the 'knee-jerk' occurred always only on the side of stimulation. Had it been reflex it ought, in accordance with the other reflexes, to have occurred on the other side.

[2] Lister, *Philosoph. Transactions*, 1858. Goltz, *Archiv für Physiologie*, Bd. viii. 1874. Vulpian, *Leçons sur l'Appareil Vasomoteur*, 1875.

branch of the facial nerve causes an increased flow of saliva from the submaxillary duct. Under normal conditions this increased flow is associated with a dilatation of the blood-vessels, but the increase can also be induced without any vascular action whatever. Atropia paralyses the secretory action of the chorda, but not its effect on the blood-vessels. From these and other data it has been established that secretion can be influenced by the nervous system primarily and directly.

The facts ascertained in reference to the innervation of the salivary secretion have been shown, by the researches of Kendall and Luchsinger[1] and other physiologists, to be true also of the secretion of sweat. Though the activity of the sudoriparous glands coincides commonly with a dilated condition of the cutaneous vessels, it has been found that even in amputated limbs, when therefore the circulation is entirely eliminated, irritation of the distal end of the nerves of the limb causes a more or less copious outpour of sweat. Similar facts may be found in clinical medicine. Copious perspiration may be seen associated with great coldness and pallor of the skin. Like the salivary secretory fibres of the chorda tympani, the perspiratory secretory fibres are paralysed by atropia, and their activity is increased by pilocarpin and other agents in a similar manner. That the centres of innervation of the sudoriparous glands exist in the spinal cord is shown by the influence of heat, dyspnœa, and reflex stimulation when the spinal cord is entirely severed from the encephalic centres.

Though the sudoriparous glands may be directly excited by certain agents, as pilocarpin, after all the nerves of a limb have been divided, yet this seems possible only for a time, and less readily than under normal conditions. The regions of spinal innervation of the sudoriparous glands seem to correspond in the main with those of general sensory and motor innervation. The paths of the secretory nerves run either directly in the spinal nerves (Vulpian) or through the sympathetic by the anterior roots, and thence again along with the ultimate ramifications of the nerves of the limb.

[1] *Archiv für Physiologie*, Bd. xiii. 1876. See also article 'Die Schweissabsonderung,' by Luchsinger, in Hermann's *Physiologie*, Bd. v.

§ 23. The influence of the spinal centres on nutrition, the so-called trophic function of the spinal cord, is especially well exemplified in the changes which occur in motor nerves and muscles when separated from the anterior horns of the cord, or when these are destroyed. The motor nerves undergo degeneration and lose their excitability. A similar degeneration occurs in the muscles, so that after the lapse of a certain interval the whole of the proper contractile substance disappears, and the muscle becomes converted into mere connective tissue. This is seen when motor nerves are diseased, or when the cells of the anterior cornua are destroyed, as in acute and chronic anterior polio-myelitis.

These trophic disorders are not explicable merely by a process of emaciation from disuse. For muscles in a state of disuse from cerebral paralysis do not undergo similar atrophic degeneration, but continue excitable, and may be maintained in a fair state of nutrition by electrical stimulation. But in the paralysis depending on disease of the anterior horns, or severance of the motor nerves, no amount of electrical stimulation will serve to maintain their contractility. They progressively lose their excitability to induced, and later to galvanic, electrical currents, and waste in spite of every effort to prevent it. These facts clearly point to a direct dependence of the normal constitution of the muscular fibres upon the healthy integrity of the anterior horns. It is practically unimportant in this relation whether the atrophic degeneration depends on irritative or inflammatory changes in the cells and efferent fibres, as held by Charcot, or on mere withdrawal of a normal trophic influence, as maintained on, I think, better grounds by Erb. The anterior horns, efferent nerves, and muscular fibre constitute a ‘ functional and nutritive unity,’ on the maintenance of which the normal structure and vital reactions of the parts composing it depend. It is not, however, necessary to assume the existence of a special set of cells and fibres called trophic as distinct from those engaged in the excitation of muscular contractions. It is more probable that the maintenance of the nutrition, and excitation of the muscles to contraction, are merely different aspects of essentially the same function.

What is true of the muscles appears to hold also in the case of the sudoriparous glands of the skin. If the degeneration does not occur to the same extent, this may be due, as Vulpian supposes, to the existence in these of peripheral ganglionic mechanisms, which are to a certain extent independent of the spinal centres.

Atrophic disorders in consequence of spinal or peripheral nerve lesions are not, however, confined to the muscles and glands, but may occur in the bones, joints, and cutaneous structures. Many of these are undoubtedly due to affection of sensory nerves and centres, rather than of the anterior horns and efferent nerves, but in many points their pathology is still a matter of uncertainty. Disturbances of cutaneous nutrition, such as herpetic eruptions, erythemata, 'glossy skin,' &c. are most frequently seen in connection with injuries of nerves and spinal centres which are accompanied by disturbances of sensation, and generally such as are indicative of irritative or inflammatory processes. They may be partly ascribed to loss of protective adaptation consequent on anæsthesia, and in some measure to vascular changes; but when all these are weighed and allowed for, there remains an element which cannot be thus explained, and which seems to justify the conclusion that the sensory centres, sensory nerves, and organs of sense, with their annexes, form a 'functional and nutritive unity,' the dissolution or disturbance of which by morbid conditions of the sensory centres or afferent nerves leads to altered nutrition or trophic disorders of the related parts. Such a mode of explanation seems sufficient to include the various trophic disorders associated with nerve lesions already mentioned, as well as the much-quoted panophthalmitis, which occurs in connection with lesion of the fifth nerve, without assuming the existence of any specific trophic centres or trophic nerves.

§ 24. If the nervous system has a direct influence on the excitation and nutrition of muscles and glands, apart from the usually concomitant vascular changes, it would follow, by implication, that the nervous system must have a direct influence on the production of heat, seeing that the muscles and glands are the chief foci of heat-production in the body.

And that in certain cases of cerebral and spinal lesion, as well as functional disorders of the nervous system of an undetermined nature, there may be abnormal heat-production of a local character out of all proportion to mere vascular dilatation—and to such an extent as, if general, would be incompatible with life—seems to be established by numerous and well-authenticated observations. But that there is a 'heat centre' which regulates the production of heat throughout the body, as distinct from the centres of motor, vasomotor, and glandular innervation, which some physiologists contend for, is neither supported by valid evidence nor is it *a priori* probable. That there is such a centre or 'point' anywhere in the nervous system, which is in afferent and efferent relations with every focus of heat-production in the body, seems to be an anatomical impossibility.

That the production of heat may be influenced by peripherical stimuli has been proved by Heidenhain,[1] Mantegazza,[2] H. C. Wood,[3] and others, apart from vasomotor change. The experiments of Tscheschichin[4] and H. C. Wood,[3] which show that after section or lesion between the pons and medulla there is a rise in heat-production which is not capable of explanation by vasomotor paralysis, are believed by the authors to indicate the existence of a centre, probably in the pons, which moderates or inhibits the evolution of heat by the foci of heat-production.

But the coarse nature of the experimental lesions, and the almost universal disorder of sensory and motor functions caused by them, together with the numerous complications involved in the conditions of prolonged observation, make such conclusions in the highest degree hazardous. It has, moreover, been proved by Bruck and Günter[5] that partial lesions, such as punctures, of the pons-medulla are more effectual in causing a rise in heat-production than complete section between the pons and medulla. This militates against

[1] Pflüger's *Archiv für Physiologie*, iii. 1870.

[2] Mantegazza, quoted by H. C. Wood, *Fever, a Study in Morbid and Normal Physiology*, 1880.

[3] *Op. cit.*

[4] *Archiv für Anat. u. Physiologie*, 1866.

[5] *Archiv für Physiologie*, Bd. iii.

the view that it is the separation of the parts below from a heat-moderating centre. The facts only allow us to conclude that injuries of certain centres and tracts cause increased heat-production, but the mode of operation is by no means satisfactorily indicated.[1]

§ 25. Though the abdominal and thoracic viscera have, in the ganglia and plexuses of the sympathetic nervous system, a more or less independent nervous mechanism, yet through the rami communicantes they are brought into afferent and efferent relations with the spinal centres and tracts. It is through these that states of the viscera are able to influence the centres of sensation, whether vaguely or in a more definite and localisable manner under abnormal conditions of irritation; and it is through the efferent branches of the anterior spinal roots that impulses are communicated from the cerebro-spinal system which regulate the calibre of the blood-vessels, the movements of the iris and hollow viscera, and the processes of secretion in the organs of digestion and assimilation (see Chap. III.)

As all the efferent nerves proceed proximately from the grey matter of the anterior cornua, the spinal centres, including those of the medulla oblongata, are the primary

[1] It is a fact that injuries also of the cortical motor centres cause rise in temperature in the paralysed limbs. This has been shown by Eulenburg and Landois, Hitzig, and H. C. Wood, and I have observed the same in my own experiments. This one would naturally ascribe to increased heat-radiation from vasomotor paralysis, which is a concomitant of the muscular paralysis. But Wood finds that there is actually increased general heat-production. If this is so, the theory that heat-production is inhibited or moderated by a centre in the pons at once falls to the ground, unless we suppose there is some still higher moderating centre. In this way we may go on to infinity.

More recently Aronsohn and Sachs ('Die Beziehungen des Gehirns zur Körperwärme und zum Fieber,' Pflüger's *Archiv*, Bd. xxxvii. Oct. 30, 1885) have shown, by a series of carefully conducted experiments, that an actual increase in heat-production is capable of being produced by puncture towards the base of the corpus striatum, or by electrical irritation of the same region No such effect can be produced by irritation merely of the cortex or subjacent medullary fibres. Their experiments indicate that the increased heat-production is dependent on irritation of certain tracts or structures, and not on paralysis of any so-called heat-moderating centre. But it by no means follows that, from these experiments, we are to assume the existence of a special heat-producing centre, distinct from those which influence the motor and vasomotor apparatus in a general sense.

centres of all the complex co-ordinations of animal and organic life. But all the functions which we ascribe primarily to the spinal centres belong also to the cerebral centres. These influence not only the muscular combinations concerned in volitional movements, but also all those functions of vascular innervation, secretion, and the like, which have their proximate centres in the spinal cord. The cerebral centres, however, control these functions only in relation with the manifestations of volition, feeling, and emotion; whereas the spinal centres, with the subordinate sympathetic system, constitute the mechanism of unconscious adaptation, in accordance with the varying conditions of ento- and epi-peripherical stimuli, which is absolutely essential to the continued existence of the organism.

CHAPTER III.

FUNCTIONS OF THE MEDULLA OBLONGATA.

§ 1. Like the spinal cord the medulla oblongata is both a path of communication between the higher centres and the periphery, and an independent centre regulating functions of the utmost importance in the system.

With the exception of the paths of volitional motor impulse comparatively little is as yet definitely known regarding the functional significance of the numerous afferent and efferent tracts which connect the medulla with the cerebellum and cerebral ganglia, or of the specific functions of the various grey centres of the medulla itself. And less has been determined in this respect by direct experiment on the medulla than by the study of secondary degeneration of the medullary tracts and the phenomena of disease. Direct experiment on the medulla itself is full of difficulties, and the results full of complications.

That the pyramids are the paths of volitional motor impulse is proved most satisfactorily by the secondary degeneration which ensues in them in consequence of destruction of the cortical motor centres (Chap. X.) The pyramid degenerates on the same side as the cortical lesion as far as the point of decussation of the pyramids, and thence the degeneration is continued downwards in the pyramidal tract of the lateral column of the spinal cord on the opposite side, and partly also in the anterior median column of the same side, for a certain distance at least. Experimental evidence as to the results of section of the pyramids is somewhat discrepant; but in monkeys and man there can be no question as to their being the motor paths between the cortex and the anterior horns of the spinal cord. This does not, however, exclude the

existence of other motor paths in the antero-lateral zones descending from the basal ganglia.[1]

Hence destruction of the pyramids does not necessarily imply total cessation of all movements in the parts below, but only of those conditioned by cortical motor impulse. If this differentiation is borne in mind many apparent discrepancies in the results of experimental investigation will completely disappear.

§ 2. As to the exact position and course of the paths of cutaneous and general sensibility, the same uncertainty, if not greater, exists as in respect to these paths in the spinal cord. But the bulk of evidence, both physiological and pathological, goes to show that they run in the medulla oblongata on the side opposite to the parts where they are distributed. Above the decussation of the pyramids, therefore, both the motor and sensory tracts of the left half of the body lie in the right half of the medulla oblongata, and *vice versa*.

So far as has yet been ascertained, the columns of Goll end in the clavate nuclei. Further connections of these tracts with higher lying centres, cerebellar or other, are therefore indirect, through the medium of the grey matter of these nuclei. The same also holds in all probability with the columns of Burdach, which end primarily in the cuneate nuclei.

The direct cerebellar tracts, as has been mentioned above (p. 14), ascend in the inferior cerebellar peduncle to the cerebellum. These tracts are clearly afferent tracts, connected with the columns of Clarke, and indirectly through these with

[1] Spitzka ('Comparative Anatomy of the Pyramid Tract,' *Journal of Comp. Med. and Surg.*, Jan. 1886) has shown that there are very considerable differences in different animals in respect to the development of the pyramids proper and their distribution. In the common type—primates, carnivora, and some rodents—the great mass of each pyramid passes into the opposite lateral column. In a second type—specially the muridæ—the great mass of the pyramid passes into the opposite posterior column. In a third—frugiverous bats—the pyramid decussates on the surface, and passes into the lateral field of the medulla oblongata.

The proboscidea and cetacea are characterised by the absence of defined pyramids in the medulla oblongata. It would seem that the tracts which correspond to the pyramids are contained in the inter-olivary layer of the reticular formation.

fibres of the spinal roots, with which they are in relation. But their functions are a matter at present only of speculation.

But neither the columns of Goll, nor the columns of Burdach, nor the direct cerebellar tracts appear to be the special paths of cutaneous sensibility, though their functions are undoubtedly sensory or afferent in some other sense. These will be considered subsequently in connection with the functions of the cerebellum (Chap. VI.)

Certain cases have been observed and investigated by Kahler and Pick,[1] Meyer,[2] Senator,[3] Spitzka,[4] and others, which indicate that the sensory tracts for the opposite side of the body run in the formatio reticularis and lemniscus of the medulla and pons on their way to the sensory regions of the cortex. It is probable that there is a decussation in the interolivary layer of tracts derived from the columns of Goll and Burdach through the clavate and cuneate nuclei, so that the whole of the centripetal tracts of the spinal cord which ascend above the medulla into the pons are in cross relations with the regions with which they are connected.

§ 3. We know much more of the functions of the medulla oblongata as an independent centre. As such it presides over and regulates functions on the due performance of which life essentially depends, as well as many others of considerable complexity but of less vital importance.

With the exception of the first four, viz. the olfactory, optic, third and fourth pairs, all the cranial nerves have their primary origin in the medulla oblongata; and the third and fourth, though springing from nuclei in the floor of the aqueduct of Sylvius, are also connected with the nuclei of the sixth pair through the posterior longitudinal tracts[5] (fig. 16, L) (Duval and Laborde).

[1] *Vierteljahrssch. f. prak. Heilkunde*, Bd. cxlii. 1879.

[2] *Archiv f. Psychiatrie*, Bd. xiii. 1882.

[3] *Ibid.* xiv. 1883.

[4] *Amer. Journ. of Neurology*, vol. ii. 1883.

[5] Pathological support of this view is given, among others, by Meyer (*Archiv für Psychiatrie*, Bd. xiii. p. 63, 1882). In a case of a hæmorrhagic focus in the right half of the tegmentum there was, along with other symptoms, paralysis of the right external rectus, with conjugate paralysis of the left internal rectus,

From this anatomical disposition alone we might infer, by analogy with the spinal centres, that the medulla oblongata would be the centre or centres of reflex co-ordination of such actions as are manifested in the regions of distribution of these nerves, singly or combined. That this is the case is abundantly proved by the facts of physiology and pathology.

Should all the encephalic centres above the medulla oblongata be removed, the mutilated organism, even of a warm-blooded animal, though deprived of the faculty of spontaneous or voluntary motion, will continue to live and breathe. The functions depending on the spinal centres will go on automatically and under reflex stimulation; and reflex actions will be called forth in regions innervated specially by the medulla itself. Thus the eyelids will close if the conjunctiva be touched; the tongue, oral and facial muscles will contract, and the ear twitch on irritation of the sensory nerves in reflex relation with the movements in question.

§ 4. But the movements capable of being elicited reflexly through the medulla oblongata are in many instances of a remarkable degree of complexity.

Thus if a morsel of food be placed on the back of the tongue the combined and co-ordinated movements of the lips, tongue, palate, and pharynx concerned in the mechanism of deglutition will be excited with as great precision as in perfectly normal conditions. In a young animal so mutilated the introduction of the nipple between the lips will be sufficient to set up the appropriate movements of sucking.

Occasionally human infants are born entirely without any cerebral centres above the medulla oblongata. Yet such anencephalous infants suck and swallow as well as the perfectly developed child when put to the mother's breast.

The medulla oblongata is the co-ordinating centre of all these associated movements. Destruction of the medulla causes their instant and permanent annihilation.

The various afferent and efferent nerves concerned in the mechanism, viz. the hypoglossal, glosso-pharyngeal, facial, and fifth, all spring directly from grey nuclei in the medulla

due to the implication of the right abducens nucleus and the fibres connecting it with the left third.

oblongata. The plexiform arrangement seen in the nerves which are concerned in the synergic movements of the limbs is not manifest in the case of the cranial nerves, except in those of the pharyngeal plexus; but there can be little doubt that here, as in the spinal centres, the nuclei of the various nerves concerned in special physiological co-ordinations are so connected together, that a co-ordinate synergy occurs on stimulation just as readily as a single muscular contraction on stimulation of an individual muscle nerve.

§ 5. The movements concerned in the production of articulate speech have also probably their primary co-ordinating centres in the medulla oblongata. This is indicated more particularly by the phenomena of disease of this region in man. In one form of disease known as *bulbar paralysis*, first defined by Duchenne, there is a gradually progressive paralysis of the tongue, lips, palate, pharynx, and larynx, so that articulation is impaired, the voice nasal; and in the end articulation, deglutition, and even phonation are altogether impossible.

The disease is found to depend on a process of degeneration specially in the nuclei of the hypoglossal, accessorio-vagus, facial and glosso-pharyngeal nerves to a greater or less extent. The order of progression of the symptoms indicates a functional association of the nuclei which are implicated, but the exact anatomical relations are still obscure. But the direct anatomical relationship between the nucleus of the abducens and the synergic muscles innervated by the third nerve, already mentioned, indicates that probably a similar connection may subsist between that of the hypoglossal and the other nuclei or nerves concerned in articulation.

Schroeder van der Kolk was of opinion that the connections of the hypoglossal and other nerves with the olivary bodies pointed to these ganglia as the co-ordinating centres of articulation. But neither anatomical nor pathological observation has rendered much if any support to this hypothesis. Vulpian has related a case in which there was complete degeneration of the olivary bodies in which articulation was unimpaired, and further researches seem rather to indicate a special relation of the olivary bodies to the cerebellum and the functions it exercises (Chap. VI.)

The medulla oblongata is a centre of facial, and of some other forms of what is usually regarded as emotional, expression. Vulpian has shown that if a young rat be deprived of all the encephalic centres above the medulla oblongata, pinching of the toes will cause not merely movements of the limbs, but also a cry as of pain. If the medulla be now destroyed pinching the toes will cause reflex movements of the limbs as before, but no cry will be elicited. The cry, as of pain, is, however, no real sign of pain, but only a reflex action of the laryngeal and expiratory muscles.

§ 6. The co-ordination of the respiratory movements is one of the most important functions of the medulla oblongata. So long as the medulla is intact the function of respiration goes on, in an automatic or reflex manner, with the most perfect regularity and rhythm. When the medulla is destroyed respiration ceases, and death ensues in all animals which cannot live by cutaneous respiration alone, like the frog.

The chief centre of co-ordination of the respiratory movements is situated near the beak of the calamus scriptorius, coinciding, or in the closest relation, with the nuclei of the vagus nerves.

This is the region termed by Flourens the *nœud vital*. From this point proceed the impulses which excite the associated and synergic movements of the diaphragm, thoracic walls, and air-passages. If the spinal cord be cut above the origin of the phrenic nerve the thoracic muscles and diaphragm speedily cease to act effectively for purposes of respiration. But, as Langendorff[1] has pointed out, these muscles may still continue to functionate rhythmically, and in response to stimulation of certain sensory surfaces for a short period after section of the cord below the calamus. In some animals respiratory movements continue for a longer or shorter period after complete removal of the medulla oblongata. But it is only through the afferent impressions conveyed by the vagi that these movements can continue in relation with the physiological necessities of the organism. The nature of the afferent impressions conveyed by the branches of the vagi distributed to the lungs and air-passages, and

[1] Du Bois-Reymond's *Archiv*, 1880.

their relation to the inspiratory and expiratory movements, is a subject on which much research has been expended, but which is still in many points scarcely definitively determined.[1] But we may regard it as fairly established that the condition of the lung at the close of expiration is the proximate stimulus to the inspiratory movements; and the distended condition of the lung, at the end of inspiration, excites the expiratory movement actively, or, by inhibiting or interfering with the inspiratory action, allows the thorax passively to collapse. The respiratory centre is in reality not a single cell group, but a bilateral group, each in relation to the vagus of its own side. The two act normally in perfect unison, but they may be divided by a longitudinal incision in the middle line, and then they lose their absolute synchronism, and each half of the respiratory apparatus may be affected independently of the other (Langendorff).

The respiratory centres are in relation, however, not only with the afferent impressions conveyed by the vagi, but also with those of sensory nerves in general, and very manifestly with those of the head and chest. Hence a sudden stimulation of these surfaces, such as by a dash of cold water or a sharp flick, causes active inspiratory action. But a sudden stimulation of any sensory surface or sensory tract has a powerful influence on the respiratory movements, and causes spasmodic arrest for the time, either in the state of inspiration or, under certain circumstances, of expiration.

The rhythmical alternation of inspiratory and expiratory movements is not, however, entirely dependent on reflex excitation; for respiratory movements may continue after all afferent nerves connected with the centre have been divided. In this case there is a true automatic activity influenced by the state of the blood itself. The diminution of oxygen and accumulation of oxidation products in the blood act as a stimulus to the respiratory centres. When the blood is artificially hyperoxygenated the movements of respiration come to a complete standstill, a condition termed *apnœa*. Non-aëration of the blood, resulting from obstruction of the respira-

[1] See on this subject Rosenthal's researches in Du Bois-Reymond's *Archiv für Physiologie*, 1880 and 1881.

tory functions, powerfully excites the movements both of inspiration and expiration; and ultimately, if the obstruction continues, causes general convulsions of the whole body, as in asphyxia. The respiratory mechanism, though essentially automatic or reflex, is to a great extent under the control of the will; for the muscles engaged in the respiratory function are also necessarily employed in many volitional acts. It is by the volitional control we possess over the respiratory movements that we are enabled to combine them with those of articulation for purposes of speech and vocalisation, and in a similar manner, by closure of the glottis and forcible contraction of the expiratory muscles, we can aid the expulsion of the contents of the rectum and genito-urinary organs. Our volitional control over the respiratory mechanism is, however, only of a limited extent. If inspiration is delayed beyond a certain point, the *besoin de respirer* becomes so urgent that voluntary effort is no longer capable of restraining the reflex or automatic activity of the respiratory centres.

Modifications of the respiratory movements are seen in the acts of sneezing, coughing, and vomiting. Irritation of the nasal mucous membrane excites a sudden inspiration, closure of the glottis, and then a forcible expiratory explosion through the nasal passages. In like manner irritation of the laryngeal or bronchial passages, or of other visceral branches of the vagus, causes a sudden explosive expiration termed a cough. Irritation of the branches of the vagus distributed to the alimentary canal, and associated conditions,[1] induce vomiting, in which there is a combination of movements, in which the essentials are dilatation of the cardiac orifice of the stomach, and forcible pressure on this viscus by the expiratory muscles of the abdomen. It is customary among physiologists to speak of a special 'vomiting centre' which co-ordinates all these movements; but the facts do not seem to me to justify such a term as distinct from that concerned in respiration, and with such modifications as are conditioned by the starting point of the exciting stimulus.

The paths by which stimuli, arriving mainly by the

[1] *Vide* a paper by the author on 'Vomiting in connection with Cerebral Disease,' *Brain*, vol. ii. 1879.

afferent branches of the vagus, centrifugally excite the respiratory muscles, are placed by Bell, and also by Schiff, specially in the lateral columns of the medulla oblongata and cervical portion of the spinal cord, which, therefore, they have termed the respiratory columns. But a large portion of the lateral columns of the spinal cord we know to be the path of transmission of motor impulses from the cerebral hemispheres; and the experiments of Vulpian and Brown-Séquard do not point to any special affection of the respiratory, as distinguished from other movements, on section of these columns. It is more probable that the centrifugal impulses from the respiratory centres pass through the fundamental spinal tracts or grey columns themselves. Mention has already been made (p. 19) of a bundle of fibres situated in the lateral ventral aspect of the vagus-accessorio-glossopharyngeal nuclei, termed by Krause the respiratory bundle (funiculus solitarius) (fig. 11, F *s*), which seems to be the path by which these centrifugal impulses travel to the diaphragmatic and other respiratory muscles. The researches of Gierke[1] show that destruction of this bundle in particular paralyses the respiratory movements.

§ 7. The medulla oblongata further exercises a controlling influence on the action of the heart and the state of the blood-pressure.

The rhythmical movements of the heart are independent of the medulla oblongata and of the cerebro-spinal centres in general, and are conditioned mainly by the intrinsic ganglia of the heart itself; though the heart-muscle contracts rhythmically on stimulation apart from all nerves or ganglia. The heart will continue to beat rhythmically after complete severance of all its cerebro-spinal connections, or even after removal from the body.

But the rate of the heart's beat is subject to variation through certain nerves connecting it with the medulla oblongata; one set of nerves inhibiting or restraining, the other accelerating or increasing the heart's action.

The inhibitory nerves of the heart run in the trunks of the vagi or pneumogastric nerves. Stimulation of the trunk of

[1] Pflüger's *Archiv f. Physiologie*, Bd. vii. 1873.

the vagus, or of the distal end of the cut trunk, or of the vagus nucleus in the medulla oblongata, causes the heart to beat slower, or stop altogether in the state of diastole. A greater or less degree of inhibition is constantly maintained by the medulla, as is shown by the acceleration of the heart's action which follows section of the vagi. The fibres which cause this inhibition of the heart spring from the spinal-accessory nucleus, and belong to the motor or centrifugal system. They terminate in the ganglia of the heart itself. How stimulation of the vagus brings about the inhibition of the heart has been a much-debated question in physiology, and still requires further elucidation. But the phenomenon seems to be essentially of the same nature as the cessation of arterial tonus (vascular dilatation) which ensues, as has been shown very clearly by Dastre and Morat,[1] when vasomotor nerves which pass into peripheral ganglia are stimulated. The normal influence exerted by the ganglia, instead of being reinforced, is interfered with; and Dr. Lauder Brunton[2] draws ingenious and suggestive analogies between this physiological interference and that which is well known in connection with waves of light and sound.

The accelerator nerves of the heart reach the heart through the last cervical and first dorsal ganglia of the sympathetic. Stimulation of these nerves, as has been proved by Gaskell, increases the strength as well as the rate of the cardiac contractions.

Both these sets of nerves are capable of being excited to activity by reflex stimulation. The inhibitory nerves may be stimulated, and the heart restrained, by powerful irritation of the sensory nerves of the surface generally; by irritation of the sensory branches of the fifth in the nostrils (Hering); by irritation of the sensory nerves of the larynx; and, in particular, by irritation of the intestinal sensory nerves. Thus a smart tap on the intestines of a frog causes the heart to stop (Goltz's experiment); a fact which serves to explain the danger of blows on the epigastrium, and the fatal consequences which, in certain conditions of the system, sometimes

[1] *Archives de Physiologie*, Nos. 2, 3, and 7, 1882.

[2] 'Nature of Inhibition,' *Nature*, 1883.

follow the sudden shock of a large draught of cold water, or irritant poison, on the sensory nerves of the stomach. The accelerator nerves can be excited reflexly by stimulation, among others, of the afferent nerves of the muscles; a fact which may partly have to do with the increased rapidity of the heart's action during active muscular exertion.

§ 8. The arterial walls are maintained in a continual state of tone, which varies within certain limits, either automatically or in reflex relation with certain local and general afferent stimuli. It has already been stated (p. 83) that the tone of the blood-vessels is in a large measure dependent on the grey matter of the spinal cord, the various segments of which may be regarded as more or less independent vasomotor centres. But a dominant influence on the vascular system, and on the variations of blood-pressure which depend thereon, is exerted by the medulla oblongata.

So long as the medulla oblongata is intact, all the centres situated above it may be removed without greatly influencing the tone of the blood-vessels, or interfering with the variations of the blood-pressure which normally occur in relation with stimulation of sensory nerves. If, however, the cord is severed below the calamus scriptorius, a general vasomotor paralysis ensues, with enormous fall of the blood-pressure, owing to the greatly increased vascular area.

It has been determined in rabbits, by the experiments of Ludwig, Owsjannikow, and Dittmar, that the region of the medulla oblongata which regulates the vascular tone extends from about three millimetres above the calamus scriptorius to within a millimetre posterior to the corpora quadrigemina; a length of about four millimetres in all. More precisely, the region, according to Dittmar, corresponds to the anterior portion of the lateral tracts, in which are scattered the ganglionic cells of the upper olive (Van Deen), or the antero-lateral nucleus (Clarke).

This region, or its homologue in other animals, is termed the vasomotor centre, and this centre is supposed to be connected with all the afferent nerves capable of modifying its influence, and, centrifugally, with every vascular area, mediately or immediately. On this point, however, there is room

for additional research. But there appears to be an undoubted direct relationship between the vasomotor centre of the medulla oblongata and the vascular area innervated by the splanchnics, and certain vascular areas of the head and neck.

The paths of the vasomotor impulses coincide with those of motor impulses in general. They leave the cord by the anterior roots, and thence in great measure pass into the ganglia and cords of the sympathetic system, through which they are distributed to the vessels directly, or through anastomosing branches which run in various cerebro-spinal nerves. The vasomotor nerves of the viscera run mainly in the great splanchnic nerves.

Those of the head and face run upwards in the cervical sympathetic, having first descended from the medulla oblongata to the anterior roots of the upper dorsal nerves, whence they pass into the sympathetic.[1]

[1] The vasomotor nerves of the head, and the dilator nerves of the pupils, seem at first sight to pursue an unnecessarily roundabout path. Having their centres in the medulla oblongata, why, one asks, should they go all the way down to the upper dorsal region of the cord before emerging to join the sympathetics, seeing that anatomically they might reach their destination in a more direct manner?

The explanation of this fact is without doubt to be sought for in embryology. I had, on purely physiological grounds, formed the speculation that the medulla oblongata should, as regards all organic functions, be looked upon as the direct continuation of the dorsal spinal cord, the cervical region being merely intercalated for the innervation of the upper extremities and their related parts.

My friend Prof. Kitchen Parker, to whom I referred on this point, kindly pointed out to me facts of development which seem to me entirely in harmony with the speculations I had formed.

Thus, in the embryo of all animals, the heart is at first in close relation with the head and the cerebral vesicles, but ultimately, as development proceeds, comes to lie at some distance posteriorly. The distance is extremely variable in different classes of animals, and depends on the number of cervical segments which are developed.

In osseous fishes, in which the cervical region is absent, the heart is in the closest relation with the head, and the first spinal (Owen, *Comp. Anat. of Vert.* vol. i. p. 307) nerve, succeeding the vagus, communicates with the second, and supplies among others the muscles of the pectoral fin, which is the homologue of the hand or arm in man.

Therefore the region of the spinal cord, which, as regards function at least, corresponds to the lower cervical or upper two dorsal segments in the monkey, comes in the fish immediately after the origin of the vagus.

In the myxine, or hag, however, the heart is situated a very considerable

§ 9. It would be natural to suppose that if the vasomotor centre exercises a more or less constant tonic effect on the walls of the blood-vessels through the sympathetic nerves, section of the sympathetic would cause vasomotor paralysis in the region to which they are distributed. Such is the case, as proved by the well-known experiments of Bernard. But the converse, viz. that irritation of the sympathetic should cause general constriction of the vessels in the same region, is only partially true. It has long been held that irritation of the cervical sympathetic causes constriction of all the vessels of the head and face. But the recent careful experiments of Dastre and Morat [1] have shown that with constriction of the vessels of the ear, and of the tongue and palate, there is marked dilatation of the vessels of the cheeks and gums. As these effects occur constantly under the same degree of stimulation, it is clear that the dilatation of the vessels is not a paralytic dilatation consequent on over-stimulation or exhaustion of vaso-constrictor fibres. This experiment has thrown great light on the mechanism of vaso-dilatation. The experiments of Bernard seemed to have established that irritation of the sympathetic always caused vaso-constriction, and that vaso-dilatation occurred only in connection with stimulation of the cerebro-spinal nerves proper, exemplified in the action of the nervi erigentes, and in the dilatation of the vessels of the submaxillary gland on stimulation of the chorda tympani.

distance posterior to the head—below the fortieth spinal segment. This has been conditioned by the development of a large number of segments for the innervation of the powerful musculature of the upper part of the body. There is every reason for believing, however, that in the embryo hag the heart at first occupies the same position in relation to the head that it does in other embryos.

As, therefore, the vagus elongates in proportion to the distance of the heart and viscera from the medulla oblongata, so also the spinal tracts which connect the vasomotor centre of the medulla oblongata with the vessels of the head and face, originally short and direct, become elongated by the intercalation of the cervical segments which are developed for the innervation of the upper extremities and their annexes. Hence they ultimately emerge by the anterior roots of the upper dorsal nerves, and reascend in the cervical sympathetic to reach their destination.

[1] 'Sur la Fonction Vaso-dilatrice du Nerf Grand Sympathique,' *Archives de Physiologie*, Nos. 2 and 3, 1882. Also their collected memoirs, *Système Nerveux Vaso-moteur*, 1884.

The facts revealed by the experiments of Dastre and Morat in the memoir above quoted, taken with those of a subsequent communication,[1] show that there is no such physiological antagonism between the two classes of nerves. Whereas stimulation of the trunk of the cervical sympathetic above the inferior cervical ganglion causes constriction of the vessels of the ear, stimulation of the anterior spinal roots of the upper dorsal region causes dilatation. Whence it appears that stimulation of the sympathetic roots below the inferior cervical ganglion suspends the constrictive action normally exercised by that ganglion, inasmuch as stimulation of the cord of the sympathetic above the ganglion causes constriction of the vessels of the ear. It is in the highest degree probable from this experiment that when vaso-dilatation occurs from stimulation of the distal end of a nerve, the effect is due to interference with the activity of peripheral vasomotor ganglionic mechanisms, of the existence of which ample evidence has been accumulated.

There would thus be a very striking analogy between the inhibition of the heart by stimulation of the vagus, and the inhibition of the vascular tone when certain nerves are stimulated. We need not suppose that there is any real antagonism between the dilators and the constrictors, but that it is merely a question of interference similar, as Dr. Lauder Brunton has suggested, to the darkness, or silence, which results when waves of light or sound fall half a wave-length behind each other.[2]

§ 10. The activity of the vasomotor centres varies with

[1] 'Les Nerfs Vaso-dilatateurs de l'Oreille Externe,' *Archives de Physiologie*, Oct. 1882, No. 7.

[2] Since this was written there has appeared an able and highly suggestive paper by Gaskell on 'The Structure, Distribution, and Function of the Nerves which innervate the Visceral and Vascular System' (*Journal of Physiology*, vol. vii. No. 1). Gaskell shows that the visceral nerves, including those that act on the blood-vessels and walls of the hollow viscera, emerge from the central nervous system in three distinct regions—the cervico-cranial, thoracic, and sacral regions. These nerves are distinguished from those of the muscles of animal life by the smallness of their calibre (varying in size from 1·8μ to 3·6μ). Their points of origin coincide with the cells of Clarke's vesicular column and their homologues, and they are probably derived from these cells. Of the visceral nerves there are two sets possessed of opposite functions, viz. motor and inhibitory—terms applicable to the vessels, heart, and hollow viscera.

The viscero-motor pass by the rami communicantes into the lateral gan-

conditions of the blood—shown more particularly in the case of asphyxia, a condition which powerfully stimulates the centres and causes vaso-constriction with great rise in the blood-pressure. They are also in reflex relation with afferent

glionic chain of the sympathetic, there lose their medullary sheath, and are so distributed to the walls of the vessels.

The inhibitory differ from the motor in not passing into the lateral ganglia of the sympathetic, but continuously onwards as medullated fibres till they reach the more distant ganglia in the tissues themselves. Here they end, lose their medulla, and are distributed as non-medullated fibres.

The inhibitory cardiac nerves of the vagus do not, like the viscero-motor branches to the thoracic portion of the œsophagus, stomach, and intestines, pass into the ganglion of the trunk of the vagus, but pass on as medullated fibres to the ganglion cells in the heart itself.

Stimulation of the viscero-motor nerves causes contraction of the visceral walls, blood-vessels, heart, and hollow viscera; while stimulation of the viscero-inhibitory causes cessation of action, such as vaso-dilatation, cardiac inhibition.

Gaskell considers that the two sets of nerves have each their special functions in the economy. The motor he terms *katabolic*, or nerves which cause increased activity and waste; the inhibitory he terms *anabolic*, or those which diminish activity and promote repair.

Among other important points in this paper it is suggested that we should regard the spinal roots, not as consisting merely of two roots—an anterior and posterior—but as consisting of three, viz. an anterior non-ganglionated root, in connection with the cells of the anterior horn; a posterior ganglionated root, in connection with the cells of the posterior horn; a lateral root divisible into (*a*) a ganglionated root, in connection with the cells of Clarke's column, and (*b*) a non-ganglionated root, in connection with the cells of the lateral horn.

Every spinal segment would be regarded as giving origin to two roots—(1) a somatic root, (2) a splanchnic root.

The somatic root is composed of two portions—a ganglionated and a non-ganglionated portion—and arises from two columns of nerve cells; viz. the cell columns of the posterior and anterior horns respectively.

The splanchnic root is composed also of two portions—a ganglionated and a non-ganglionated portion—and arises also from two columns of cells; viz. the column of Clarke and that of the lateral horn. The ganglia of the splanchnic roots are the ganglia of the sympathetic chain, and are homologous with the ganglion trunci vagi.

In respect to the non-ganglionated portion of the splanchnic root Gaskell points out that in the case of the spinal accessory, where the distinction between the somatic and splanchnic roots is specially apparent, this root (the external) is distributed to the sterno-mastoid and trapezius muscles, besides sending a branch to the cervical plexus.

The internal branch, which is derived from the lateral horn, and is composed of small medullated fibres, is the visceral branch, and goes to the ganglion trunci vagi. He shows that the distribution of the non-ganglionated portion of the splanchnic root harmonises with Sir Charles Bell's hypothesis of the existence of lateral or respiratory roots—as distinct from the sensory or

nerves which excite or depress their activity—pressor and depressor nerves as they are sometimes respectively termed.

Stimulation of sensory nerves in any part of the body excites the vasomotor centres and causes constriction of the vessels. The paths of the afferent impulses which so act coincide, according to the researches of Miescher, Ott, &c. with those of sensation in the spinal cord, viz. the postero-lateral tracts. But along with the general excitation of the vasomotor centres, there is local dilatation at the point stimulated, as is well seen in the redness of the skin which follows irritation from any cause (Lovén). A similar local dilatation of the vessels of the stomach is observed on irritation of the gastric branches of the vagus (Rutherford).

Irritation of the cerebral end of a certain branch of the vagus, which joins the cardiac plexus, has the effect of producing a great fall of the blood-pressure by causing dilatation, more particularly of the splanchnic vascular area. This nerve has received the special name of the depressor nerve (Ludwig and Cyon). Apparently this nerve is thrown into action by distension of the ventricular cavities, and laboured action

posterior and the anterior or common motor—containing nerves which excite motions dependent on, or related to, the act of respiration.

'I imagine,' says Sir C. Bell, 'that the same column or tract which gives origin to the fourth, seventh, glosso-pharyngeal, par vagum, and spinal accessory nerves is continued downwards along the lateral parts of the spinal marrow, and that it affords roots to the spinal nerves, constituting them respiratory nerves, as well as nerves of motion and sensation; and that it especially supplies the roots of the diaphragmatic nerve and the external respiratory nerve.'

This view is further supported by Van Wijhe's embryological researches, which indicate a separation of the muscles of the head into two groups, according as they are developed from the mesoblastic somites or the lateral plates. The muscles formed from the somites are the muscles of the eye supplied by the third, fourth, and sixth nerves, and those supplied by the hypoglossal; while those of the jaw and mastication are derived from the lateral plates, i.e. from the walls of the visceral clefts. These correspond in the main to Bell's respiratory system. If this differentiation is maintained throughout the skeletal muscles generally there would be grounds for assuming that the non-ganglionated portion of the somatic root supplies all the muscles of the somatic skeleton, i.e. muscles derived from the mesoblastic somites or myotomes; while the non-ganglionated portion of the splanchnic or lateral root supplies the muscles of the visceral skeleton, i.e. those derived from the lateral plates of the mesoblast, or, in other words, from the mesoblast of the walls of the visceral clefts.

of the heart, and thus fall of the blood-pressure and relief of the vascular tension, are brought about. By the reciprocal relations which subsist between the centres of innervation of the heart and blood-vessels variations in the blood-pressure are kept within limits. A dilated condition of the blood-vessels, which causes great lowering of the blood-pressure, and would thus seriously affect the circulation, is compensated for by an increased activity of the heart. So a contracted state of the blood-vessels, causing great rise in the blood-pressure, is counteracted by inhibition or slowing of the heart. By these means great variations from the normal standard are prevented.

All these automatic and reflex regulative adaptations in the circulatory system are capable of being maintained in their integrity in the entire absence of all the encephalic centres situated above the medulla oblongata, and cease when the medulla is destroyed. The medulla oblongata is thus a co-ordinating centre of reflex actions essential to the maintenance of life. If all the centres above the medulla oblongata be removed, life may nevertheless continue. The respiratory movements may go on with their accustomed regularity and rhythm; the heart will continue to beat and the circulation be regulated as under normal conditions; the animal may swallow if food be placed in its mouth, may react in an apparently purposive manner to impressions made on its sensory nerves, withdrawing its limbs or endeavouring to remove itself from the cause of irritation, or even utter a cry as of pain, and yet will be merely an unconscious, unintelligent reflex mechanism.

Note.—Though this work does not deal with the symptoms of disease or injury of the nerve centres, except in so far as they throw light on or illustrate their physiology, special mention seems required of certain results which are observed in connection with lesions of the medulla oblongata. Apart from all disturbances of the great vital functions regulated by the medulla oblongata, a remarkable fact was discovered by Claude Bernard in reference to the influence of lesions of the floor of the fourth ventricle on the processes of assimilation and excretion. He found that puncture of the fourth ventricle, in the neighbourhood of the nuclei of the vagi,

caused a condition of diabetes, sugar appearing in large quantity in the urine.

The investigations in particular of Cyon and Aladoff[1] have shown that this formation and excretion of sugar is a secondary result of the vasomotor paralysis of the liver, which is the immediate consequence of the lesion in question. The vasomotor innervation of the liver being dependent on the medulla oblongata, lesions of the medulla oblongata necessarily, among other results, cause disturbance of the circulation and glycogenic function of the liver. Such being the rational explanation, it seems absurd to speak of a 'sugar-forming centre' in the medulla oblongata. The centre is the vasomotor centre; all the pathological phenomena are mere secondary consequences of the disturbance of a great and important physiological mechanism.

So also in respect to another series of pathological phenomena which result from certain lesions of the medulla oblongata. It has been found that general convulsions occur when the medulla oblongata is irritated by the blood of asphyxia, or, which comes to the same thing, by total bloodlessness (Kussmaul and Tenner's anæmic convulsions); as also by lesions of the upper portion of the floor of the fourth ventricle (Nothnagel). These are all obviously dependent on abnormal irritation of the centres and tracts which have definite physiological functions to perform. To speak of such phenomena as indicating the existence of a 'convulsion centre' is, in my opinion, a most reprehensible abuse of physiological terms.

[1] *Bulletin de l'Académie Impériale de St. Pétersbourg*, tome viii.

CHAPTER IV.

FUNCTIONS OF THE MESENCEPHALON AND CEREBELLUM.—GENERAL.

§ 1. We may now proceed to the consideration of those parts of the encephalon which lie between the cerebral hemispheres and the medulla oblongata. It will be advantageous to consider them first in their totality, and next as regards their individual functions, in so far as these are capable of differentiation from each other.

We have already briefly discussed the actions of which an animal is capable in which all the centres above the medulla oblongata have been removed, and we have endeavoured to allot to the medulla and cord the functions proper to each. In a similar manner the functions of those parts of the encephalon now under consideration may be determined by a study and analysis of the forms of activity which are manifested by animals, from which all the centres situated in advance of the optic thalami and of the optic lobes have been removed.

Of experiments of this kind multitudes have been performed, with a tolerably uniform agreement as to results; though, as regards their interpretation and significance, there is not the same unanimity of opinion. It is to the researches of Flourens [1] and Longet [2] that we owe our chief knowledge of the results of ablation of the cerebral hemispheres, though much has been added by subsequent investigators, mainly of the French school of physiology, prominent among whom stands Vulpian.[3]

[1] *Recherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux*, 2nd ed. 1842.

[2] *Traité de Physiologie*, 2nd ed. 1866.

[3] *Leçons sur la Physiologie du Système Nerveux*, 1866.

The phenomena manifested by animals deprived of their cerebral hemispheres vary considerably in the different classes of vertebrate animals; differences which mainly depend on the degree of solidarity, as Vulpian well expresses it, which subsists between the individual centres of the cerebro-spinal system, according as we ascend or descend the animal scale.

§ 2. In the case of the frog[1] deprived of its cerebral hemispheres (A, fig. 43), the following are among the chief phenomena which are observed. Deprived of its cerebral hemispheres, the frog will maintain its normal attitude, and resist all attempts to displace its equilibrium. If laid on its back, it will immediately turn on its face, and regain its station on its feet. If placed on a board, and the board be tilted in any direction, the animal will make the appropriate bodily movements to throw its centre of gravity within the base of support. If its foot be pinched, it will hop away. If it is thrown into the water, it will swim until it reaches the side of the vessel, and then clamber up and sit perfectly quiet. If its back be stroked gently, it will utter loud croaks, and this with such uniformity on each application of the stimulus that, as Goltz indicates, a chorus of brainless frogs might be obtained which would utter their *βρεκεκεκέξ κοάξ κοάξ* on the appropriate occasion in a manner which would have delighted the heart of Aristophanes. Indeed, in many respects, it would be difficult to say that the removal of the hemispheres had caused any alteration in the usual behaviour of the animal. If placed in a vessel of water, the temperature of which is gradually raised, it will not quietly submit to be boiled like a frog which has only its medulla and spinal cord, but will leap out as soon as the bath becomes uncomfortably hot. If placed at the bottom of a pail of water, it will ascend to the surface to breathe. And not merely so, but if placed in a vessel inverted over a pneumatic trough, and containing a column of water sustained by barometric pressure, it will ascend to

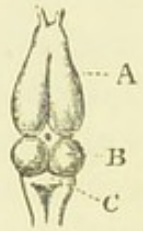


FIG. 43.—Brain of Frog. A, cerebral hemispheres. B, optic lobes. C, cerebellum.

[1] On this subject see particularly the researches of Goltz—*Functionen der Nervencentren des Frosches*, 1869.

the surface as before; but not finding there the necessary atmospheric air, it will work its way downwards, and succeed in making its escape out of the vessel to the free surface of the trough. There is a method in its movements. If an obstacle be placed between it and the light of a window, the frog will not spring blindly against the obstacle when its toe is pinched, but will clear it, or spring to the side. It will alter the course of its leap according to the position of the obstacle between it and the light. There is, so far, no difference between its behaviour and that of a frog in full possession of all its faculties. But yet a very remarkable difference is perceptible. The brainless frog, unless disturbed by any form of peripherical stimulus, will sit for ever quiet in the same spot, and become converted into a mummy. All spontaneous action is annihilated. Its past experience has been blotted out, and it exhibits no fear in circumstances which otherwise would cause it to retire or flee from danger. It will sit quite still if the hand be put forth cautiously to seize it, but will retreat if a brusque movement is made close to its eyes. Surrounded by plenty it will die of starvation; but, unlike Tantalus, it has no psychical suffering, no desire, and no will to supply its physical wants.

§ 3. The results which have been observed in fishes after similar ablation of the cerebral hemispheres (A, fig. 44), are, *cæteris paribus*, of the same nature as those seen in frogs. A fish so mutilated maintains its normal equilibrium in the water, and uses its tail and fins in swimming with as great precision and co-ordination as before. The brainless fish is, however, continually on the move, and there is also method in its movements. It will not run its head against any obstacle placed in its path, but turn to the right or left according to circumstances. Left to itself in the water, it swims in a straight line, and, unlike other fishes which loiter by the way, smelling at this and nibbling at that, it keeps on its course, as if impelled by some irresistible impulse, and only stops when it reaches the side of the vessel, or when worn out by pure nervous and muscular fatigue. Apparently there is

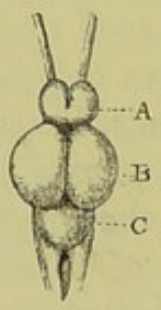


FIG. 44.—Brain of Carp. A, cerebral hemispheres. B, optic lobes. C, cerebellum.

some essential difference between the frog, which sits for ever quiet, and the fish which goes on indefinitely, but the same explanation is applicable to both (p. 115).

Like the frog, the fish perishes of starvation, surrounded by abundant supplies of otherwise tempting food.

§ 4. The results of removal of the cerebral hemispheres in pigeons have been described in great detail by Flourens, Longet, Vulpian, &c. A pigeon so mutilated continues able to maintain its equilibrium, and to regain it when disturbed. When placed on its back it succeeds in regaining its feet. When pushed or pinched it marches forward. Should it happen to step over the edge of the table it will flap its wings until it regains a firm basis of support. When thrown in the air it flies with all due precision and co-ordination. Left to itself it seems as if plunged in profound sleep. From this state of repose it is easily awakened by a gentle push or pinch, and looks up and opens its eyes. Occasionally, apparently without any external stimulation, it may look up, yawn, shake itself, dress its feathers with its beak, move a few steps, and then settle down quietly, standing sometimes on one foot and sometimes on both. Should a fly happen to settle on its head it will shake it off. If ammonia be held near its nostrils it will start back. Should the finger be brusquely approximated to its eyes, it will wink and retreat. A light flashed before its eyes will cause the pupils to contract; and if a circular motion be made with the flame, the animal may turn its head and eyes accordingly. It will start suddenly and open its eyes widely if a pistol be discharged close to its head.

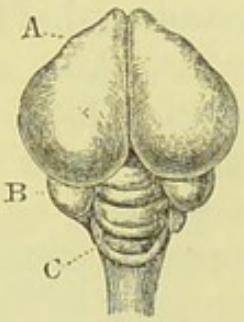


FIG. 45.—Brain of the Pigeon. A, cerebral hemispheres. B, optic lobes. C, cerebellum.

After each active manifestation called forth by any of these methods of stimulation, the animal again subsides into its state of repose. It makes no spontaneous movements. Memory and will seem annihilated. When irritated it may show fight both with wings and beak, but it exhibits no fear and makes no attempts at escape. It resists attempts to open its beak for the purpose of introducing nourishment, but should its resistance be overcome, it swallows as usual. If fed artificially

it may be kept alive for months,[1] but left to itself it will die of starvation, like the frog or fish.

§ 5. When we pass from the consideration of the functions which the lower centres in frogs, fishes, and birds are capable of performing, independently of the cerebral hemispheres, to the effects of removal of the hemispheres in mammals, we have to deal with phenomena of a more varied character. We have seen that frogs, fishes, and birds, deprived of their cerebral hemispheres, continue to perform actions in many respects differing little, if at all, from those manifested by the same animals under absolutely normal conditions. But the results, in the case of mammals, are far from exhibiting the same degree of uniformity. Differences of a marked character exist, according to the age of the animals experimented on, and the order to which they belong. If we were to draw conclusions from experiments on one order of animals, and extend them, without due qualification, to animals in general, and particularly to man, we should be in danger of falling into serious errors. The neglect of such considerations has been a fruitful source of discrepancies and contradictions between individual physiologists, and between the facts of experimental physiology and those furnished by clinical and pathological research.

Though we may take it as a reliable guide in our inquiries, that nerve centres constructed on the same type perform homologous functions, yet, as we ascend the animal scale, the centres of which the cerebro-spinal system is composed become more and more intimately bound up and associated with each other in action, so that to separate the one from the other involves such functional perturbation of the whole that only in rare instances is it possible to obtain indications of independent activity on the part of those which are not directly injured. That such is the case will be abundantly illustrated as we proceed.

Among mammals, rabbits and guinea-pigs have been the

[1] McKendrick, however, shows that the complete extirpation of the basal ganglia along with the hemispheres proper is not compatible with long survival ('Experiments on the Corp. Striat. and Cerebral Hemispheres of Pigeons,' *Trans. Roy. Soc.* Edin. 1873.

favourite subjects of physiological research; and of these, those of tender age are best adapted for the purpose, on account of the lesser degree of solidarity which subsists between their several encephalic ganglia as compared with those of a more advanced age. Removal of the hemispheres exerts less general functional disturbance in them than in those which have reached a greater degree of maturity, a fact of no small importance in relation to the progressive evolution of intelligence. But even in adult rabbits the lower centres rapidly regain their power of independent action, after the first shock caused by the removal of the hemispheres has subsided.

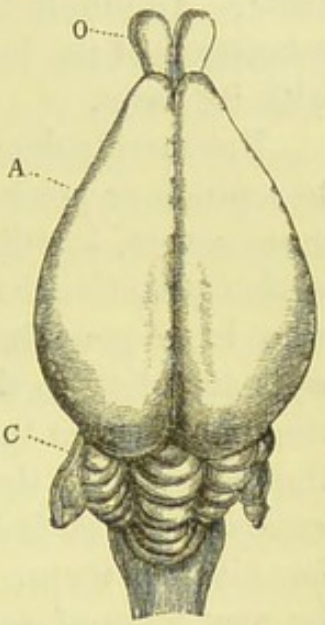


FIG. 46.—Brain of the Rabbit. A, the smooth cerebral hemispheres. O, the olfactory bulbs. C, the cerebellum.

When the hemispheres have been removed from a rabbit (A, fig. 46) or guinea-pig, the animal, at first utterly prostrate, after a varying interval begins to show signs of the retention of a capacity for the performance of actions of a considerable degree of complexity. It is observable, in the first place, that the muscular power of the limbs has become enfeebled to a noteworthy extent. The muscular weakness is proportionately much more marked in the fore than in the hind limbs. The animal can maintain its equilibrium on its legs, though of a rather unsteady character, and the fore paws have a tendency to sprawl, or to be planted in irregular positions. If the equilibrium is disturbed the animal is capable of regaining it. If the hind foot is pinched the animal will bound forward in the usual manner, until it strikes its head against some obstacle, or until the excitation has exhausted itself.

It is very doubtful whether rabbits are able to avoid obstacles in the path like frogs and fishes similarly treated.

The pupils, however, still contract when a strong light is thrown into the eye, and the eyelids wink if the conjunctiva is directly menaced. A loud sound will cause the ear to twitch, and provoke a sudden start. Colocynth, or some other equally

unpleasant sapid stimulus, will cause movements of the tongue and muscles of mastication in all respects resembling those characteristic of disgust, with efforts to get rid of the nauseous taste. Ammonia held before the nostrils will cause a sudden retraction of the head, or induce the animal to rub its nostrils with its paws.

Not merely does the animal respond by certain movements to a pinch or prick of its toes or tail, but if the pinch is a little more severe, it will respond with repeated and prolonged cries of that plaintive character with which all sportsmen are familiar who have gone hare or rabbit shooting. Vulpian[1] specially calls attention to the plaintive character of these cries as distinguished from the brief cry which may be elicited when all the parts above the medulla have been destroyed. My own experiments entirely confirm the description which Vulpian has given of them. If the animal be left to itself, undisturbed by any form of external stimulus, it remains fixed and immovable on the same spot, and, unless artificially fed, would die of starvation, like the frog, fish, and bird, in the midst of plenty, even if the severity of the operation did not, as it generally does, speedily induce a fatal issue.

With the exception of the greater degree of muscular paralysis and the diminished power of accommodation of movements in accordance with sensory impressions in general, and with visual impressions in particular, the phenomena manifested by rodents deprived of their cerebral hemispheres differ little from those already described in frogs, fishes, and birds. The power of maintaining the equilibrium is retained, co-ordinated locomotive actions and emotional manifestations are capable of being excited by impressions on sensory nerves, essentially if not altogether to the same extent in all. In cats, dogs, and higher animals the prostration is so great, and there

[1] Vulpian states that station, locomotion, &c. are possible in young rabbits in which all the centres above the corpora quadrigemina have been removed. Christiani (*Physiologie des Gehirns*, 1885) contends also that they are able to avoid obstacles after removal of the cerebral hemispheres. In his operations the optic thalami are, however, left uninjured, only the hemispheres and the corpora striata being removed. Under such circumstances it is not improbable that there may be responsive actions in accordance with retinal impressions, similar to those manifested by frogs and fishes.

is such interference with motor power, that the independent activity of the lower centres, as far as relates to the maintenance of equilibrium and co-ordinated progression, practically ceases to exist; though the fact of emotional response to sensory impressions points to the conclusion that we have to deal, not with the complete absence, but only with the suspension of the other forms of functional activity. This conclusion is capable of substantiation by other facts, to be adduced when we come to consider in a more detailed manner the functions of the hemispheres.

§ 6. When we turn from the consideration of the facts themselves to the theory of their explanation, we enter on a *quæstio vexata* of physiology and psychology.

One fundamental fact, however, seems to be conclusively demonstrated by these experiments, viz. that in the absence of the cerebral hemispheres the lower centres, of themselves, are incapable of originating active manifestations of any kind. An animal with brain intact exhibits a varied spontaneity of action not, at least immediately, conditioned by present impressions on its organs of sense. When the hemispheres are removed, all the actions of the animal become the immediate and necessary response to the form and intensity of the stimulus communicated to its afferent nerves. Without such excitation from without the animal remains motionless and inert. It is true that some of the phenomena which have been described would seem to be opposed to this view, but they are so in appearance only and not in reality. Thus, we have seen that a frog may occasionally move its limbs spontaneously, and a bird may yawn, shake its feathers, or change its foot; but these actions are the result of impressions arising from cutaneous irritation or internal discomfort—'ento-' or 'epi-peripherical' impressions—or in some cases from the irritation caused by the wounded surface resulting from the operation.

The same law satisfactorily accounts for the immobility of the frog on land, and the activity of the fish in water. In the one case there is no external source of irritation, in the other the contact of the mobile water with the body surface acts as a continual external stimulus to the natatory

mechanism. As this is constant, so the fish continues to swim until arrested by some insurmountable obstacle or by pure nervous or muscular fatigue. We have only to throw the frog into the water to complete the proof. The frog, like the fish, will continue to swim until it reaches dry land or becomes exhausted. Hence the phenomena manifested by the different classes of animals after ablation of the hemispheres admit of generalisation under the law that the lower ganglia are centres of immediate responsive action only, as contradistinguished from the mediate or self-conditioned activity which the hemispheres alone possess.

§ 7. We have next to inquire, What is the nature of the impression which is the immediate antecedent of this responsive activity? Is it a purely physical phenomenon, or has it likewise a subjective side? In other words, are these actions merely reflex or excito-motor, or are they accompanied by sensation properly so called? If we define sensation as the consciousness of an impression, it will be seen that the problem to be solved is, whether consciousness is an accompaniment of the activity of these centres, and whether, therefore, we have here to deal with truly psychical phenomena. I have already, in discussing the functions of the spinal cord, observed that the existence or not of consciousness in others than ourselves is entirely a matter of inference or testimony. In the lower animals we can only judge from the character of the phenomena they manifest, and by analogy with our own actions. If it is difficult to determine the nature of the adaptive faculty of the spinal cord, it is not the less difficult in regard to the centres now under consideration. If we adopt the metaphysical view, that mind and consciousness form an indivisible unity, and that annihilation of one great class of mental manifestations necessarily involves the annihilation of mind as a whole, seeing that the indivisible cannot be divided, it would be easy to argue that, as the ablation of the hemispheres abolishes certain fundamental powers of mind, therefore the functions of the lower centres must be outside the sphere of mind proper. But this way of looking at the subject will not harmonise with the facts of physiology, for, as we shall find when we come to discuss the functions of

the hemispheres, whole tracts may be completely and irrevocably cut out of the territory of intellectual consciousness without interfering with the integrity of consciousness *qua* others; and will may be abolished while consciousness remains. Hence we are not entitled to say that mind, as a unity, has a local habitation in any one part of the encephalon, but rather that mental manifestations in their entirety depend on the conjoint action of several parts, the functions of which are capable, within certain limits, of being individually differentiated from each other. If we have regard merely to the character of the reactions which result from impressions made on the various organs of sense, it will be found impossible to distinguish between them and those which are actuated by a distinct consciousness of the impression. Thus, a severe pinch on the tail or foot of a brainless rabbit elicits not merely convulsive reflex movements, such as may result from the activity of the spinal cord alone, but calls forth the repeated and prolonged cry which is characteristic of pain. The frog, in like manner, would appear to have a distinct sense of pain when it makes frantic efforts to escape from its hot bath. And it would seem to be a consciousness of retinal impressions which causes the frog, when urged to move, to leap aside so as to avoid an obstacle placed in its path; or which causes the fish, under similar circumstances, to deviate sharply from the straight course which it would otherwise pursue. But we cannot rely on appearances alone. For, on the other hand, it may be that the mesencephale is a centre of reflex reaction of a special form, differing from the spinal cord not in kind, but only in degree of complexity. Just as the medulla oblongata is a centre of more complex and special coordination than the spinal cord, so the mesencephale may be the centre of still more complex special reflex actions, among which may be the reflex expression of emotion. Hence the plaintive cry elicited by pinching the foot of a rabbit may be merely a reflex phenomenon, not depending on any true sense of pain. And so the leap to the side which the brainless frog makes so as to avoid an obstacle would be merely the resultant of two simultaneous impressions, the one on its foot and the other on its retina.[1] Lotze also argues that even though such

[1] *Göttingische Gelehrte Anzeigen*, 1853, quoted by Goltz, *op. cit.*

apparently intelligent reactions should not be conditioned by the primary constitution of these nerve centres, they may be the result of an organic nexus established between certain impressions and certain actions by the past experience of the animal under similar circumstances ; that which was primarily a conscious action becoming by frequent repetition a reflex action of a secondary character. Of this conversion of conscious action into secondary reflex, numerous other examples might be quoted. This view, however, will not of itself suffice to account for all the phenomena.

By a series of ingeniously contrived experiments, Goltz has shown that, even when the limbs of a frog were so fixed or placed in positions which could never have occurred in its past experience, the animal, without its hemispheres, retained the power of adapting its movements in accordance with these unusual and abnormal conditions. This would indicate that if these centres are centres merely of reflex action, the reaction is that of a machine possessing in some way the power of self-adjustment.

But the mere faculty of adaptation is not necessarily a proof of consciousness, for, as we have seen, it exists in some degree in the spinal cord, and if it is not regarded as proof of conscious action on the part of the cord, neither can it be taken as such here ; for it may be that the more complex adaptation manifested by the mesencephale is simply the result of more complex and special afferent and efferent relations. On this supposition we might account for the difference which is observed in the behaviour of two frogs, the one retaining its mesencephale and cerebellum, the other only its cord, when placed together in a vessel of water, the temperature of which is gradually raised. The mechanism of leaping possessed by the one may be set in action by a stimulus which is not sufficient to excite convulsive reaction through the spinal cord of the other. And that this may be so is rendered more probable by another important fact observed by Goltz, viz. that the reflex movements of the limbs of the decapitated frog can be excited in the usual manner (*e.g.* by chemical irritation) during the continuance of the heat which is already causing the other to make efforts to escape. We cannot,

therefore, rely on the phenomena of adaptation as indisputable proof of the existence of consciousness. Carpenter, who with Longet regards the mesencephale as the *sensorium commune* or seat of sensation, and terms the reaction of these centres *sensori-motor* reaction, adduces in support of the existence of consciousness the evidently conscious actions of invertebrate animals, which have no true cerebral hemispheres, but only a series of ganglia homologous with the mesencephalic ganglia of vertebrates.

This would be a powerful argument if the cases were in other respects quite parallel. But it is materially weakened by the fact that invertebrate animals are capable of actions of an entirely *different kind* from those of vertebrates deprived of their cerebral hemispheres.

These animals manifest a varied spontaneity of action under, as far as we can see, the same external conditions; they seek their food, are capable of education, and learn to adapt their actions so as to seek what is pleasant and avoid that which is painful; faculties which are entirely abolished by removal of the cerebral hemispheres in vertebrates.

From this I would argue that the ganglia of the invertebrates are not completely homologous with the mesencephalic ganglia of vertebrates; for if they were so, we should expect that not merely sensation, but also the other psychical faculties, should be manifested by vertebrates deprived of their cerebral hemispheres, even though to a less degree. But it is not a difference in degree only which is observed, but a manifest difference in kind. It is probable, therefore, that in the ganglia of the invertebrates there are nerve cells which perform, in however lowly a manner, the functions of the cerebral hemispheres in vertebrates.

The fact of consciousness being correlated with the activity of the mesencephale still, therefore, as far as relates to experiments on the lower animals, remains undecided. It is more easy to ascertain the conditions of consciousness in ourselves. The only proof of consciousness of an impression, except for the immediate present, is the fact that we remember it. Without some degree of persistence in memory, sensation practically has no psychical import; without memory to serve

as a basis of comparison between past and present there can be no perception, and no rational or intelligent action founded on impressions received by our organs of sense. It is usual to regard the hemispheres as the seat of memory and perception, but the question still remains whether the hemispheres are necessary for sensation or consciousness of impressions of the moment.

We obviously cannot obtain any answer to the question, when the functions of the hemispheres are so affected as to prevent the expression in words or by gesture language of subjective states, if any such really exist. But we have experiments of disease which practically detach the hemispheres from their mesencephalic connections, and leave thought and speech intact, so that we can obtain direct testimony as regards the consciousness of impressions. Such an experiment is performed by a lesion of the crus cerebri or of the posterior part of the internal capsule (see Chap. IX.), phenomena not unfrequently occurring in clinical experience. When this occurs, the individual has absolutely no consciousness of tactile impressions made on the opposite side of his body, *however much he may strain his attention to receive them.* In the mesencephale alone, therefore, sensory impressions are not correlated with modifications of consciousness; whence we must conclude that sensation is a function of the higher centres. The results of experiments on monkeys, to be subsequently detailed, are quite in accordance with those of disease in man. We may conclude from the homology of the mesencephale of man with that of the lower vertebrates that the functions are of the same type, and only differ in degree of independence; and therefore I would refuse the term sensation, in its acceptation as the consciousness of an impression, to the receptivity of the mesencephalic centres. But how are we to designate this self-adjustable respondence to sensory impressions? Flourens, with whom I agree, was of opinion that sensation proper was abolished by removal of the cerebral hemispheres. Vulpian qualifies the term sensation, ascribed to the mesencephale by Longet and Carpenter, by the adjective '*crude*' or '*obscure*,' in contradistinction to the '*distinct*' sensation or '*perception*,' as he terms it, of the cerebral hemi-

spheres. Goltz, without deciding the question positively, in one way or the other, ascribes to the mesencephale an '*adaptive faculty*' (Anpassungsvermögen), and terms the reactions of these centres '*responsive movements*' (Antwortsbewegungen), terms which I have adopted and frequently employed. Huxley would call a sensory modification which is not correlated with consciousness a *neurosis*, and one which has also a subjective aspect a *psychosis*, terms which might be employed, but for the disadvantage of neurosis being used in medicine to signify a diseased function of nerve. If we avoid the term sensation altogether, and arbitrarily use the term *æsthesis* to signify a mere physical impression on the centres of special sense, and the term *noesis* to signify a conscious impression, we may avoid some of the difficulties caused by the ambiguities involved in the common terms. The reaction of the mesencephalic and cerebellar centres might be termed *æsthetiko-kinetic*, and be thus distinguished from the *kentro-kinetic* or excito-motor action of the spinal cord on the one hand, and the *noetiko-kinetic* action of the cerebral hemispheres on the other.

Having thus far considered the general character of the functions of the mesencephale and cerebellum apart from the cerebral hemispheres, we have next to inquire more specially into the individual forms of functional activity, with the view, if possible, of determining the mechanism and central localisation of each.

We may classify the functional manifestations already described under three heads:—1. Equilibration, or maintenance of the bodily equilibrium. 2. Co-ordination of locomotion. 3. Emotional expression. The first and second of these are so intimately bound up together that the consideration of the one implies, more or less, the consideration of the other.

I. The Maintenance of Equilibrium.

§ 8. That this is a function of the mesencephalic and cerebellar centres is clearly demonstrated by Goltz's balancing experiments on frogs and birds, already described. It has been seen that an animal, deprived of its cerebral hemispheres, is capable not only of maintaining its equilibrium, if undis-

turbed, but of regaining it when overthrown. It can incline the head and body in such a manner, when the basis of support is tilted, as to keep the centre of gravity within the base. Considerable diversity and complexity of muscular movements, all adapted for this purpose, are called into play, according to the conditions under which the animal may be placed. A frog placed on an inclined plane of steep gradient is impelled, as it were, irresistibly to climb up, in order to prevent itself falling backwards. A pigeon accidentally stepping off the table into thin air is irresistibly urged to flap its wings, to sustain itself until it regains *terra firma*. Mammals deprived of their cerebral hemispheres retain the same power, though to a less marked extent; the various orders of animals differing much in this respect.

The maintenance of the equilibrium is an example of æsthetiko-kinesis, and involves the conjoint operation of three separate factors:—1. A system of afferent nerves and organs. 2. A co-ordinating centre. 3. Efferent tracts in connection with the muscular apparatus concerned in the action. The faculty of equilibration is overthrown by lesions of the afferent apparatus alone, or by lesions of the encephalic centre alone, or by lesions of the efferent tracts alone, or by conjoint lesion of all. Various degrees and forms of perturbation of this function will result, according to the nature and extent and position of the lesion. In many respects the maintenance of the equilibrium resembles the tone of muscles. Lesions of the afferent nerves, central ganglia, or motor nerves destroy the tone of muscles; and, according as this occurs in both or only in one group of antagonistic muscles, we have complete muscular flaccidity or extensor, flexor, or lateral distortion. So, in regard to equilibrium, similar lesions may cause complete overthrow, or various forms of distortion exhibited as reeling, staggering, rotation, and the like.

The afferent apparatus is of a compound nature, but mainly consists of three great systems, which in conjunction form that synæsthesis on which the due maintenance of equilibrium and co-ordination depend. The equilibrium is disturbed by lesions of one or more, or all, of these. These three systems are—1. Organs for the reception and transmission of tactile

or common sensory impressions. 2. Organs for the reception and transmission of visual impressions. 3. The semicircular canals of the internal ear, and their afferent nerves.

The Influence of Tactile Impressions.

§ 9. That these form an integral factor in the general consensus is demonstrated both by direct experiment and by the facts of pathology.

We have already seen that a frog deprived of its cerebral hemispheres, but in which the optic lobes and cerebellum are intact, still retains the power of maintaining its equilibrium, and adapting its movements to this end, under diverse conditions. If, now, the skin be removed from the hinder extremities, the animal at once loses this power, and falls like a log when the basis of support is tilted. The removal of the skin has destroyed the receptive organs of those sensory impressions which are necessary to excite the co-ordinating centre to the adjusted combinations of muscular action requisite for equilibration. The sensory nerves of the denuded surface are not of themselves capable of conveying the proper stimulus to the co-ordinating centre. This is a fact in harmony with the law laid down by Volkmann, and confirmed by all subsequent observers, that reflex reactions are more capable of being excited by impressions on the *cutaneous* extremities of afferent nerves than by stimuli applied to any other part of their course.

A similar result ensues in man, as has been shown by Heyd,[1] when the soles of the feet are rendered insensible by chloroform or refrigeration. When this is done there is great difficulty in maintaining the equilibrium when the eyes are shut, and the individual oscillates and sways in a very pronounced manner.

In the disease known as tabes dorsalis, or locomotor ataxy, dependent on sclerosis of the posterior columns of the spinal cord, one of the characteristic symptoms, in addition to the locomotor inco-ordination, is the difficulty or absolute impossibility of maintaining the equilibrium when the eyes are shut.

[1] Heyd, *Der Tastsinn der Fusssohle als Aequilibrirungsmittel des Körpers*, 1862.

This is seen particularly when the individual tries to stand with his feet close together and his eyes shut. He oscillates greatly, or actually falls if unsupported. So also it is difficult or altogether impossible for him to stand or walk in the dark though the eyes are open.

In this disease there is usually a numbness in the soles of the feet, with diminution or entire absence of sensibility to tactile impressions, so that the patient feels as if something soft were interposed between his feet and the ground, or he does not feel the ground at all.

The individual so affected may, however, retain his voluntary motor power, and can move his limbs freely and forcibly in the recumbent posture, or even direct the movement of his lower extremities without any appreciable lack of precision. As a rule, the difficulty in maintaining the equilibrium is associated with ataxy of movement, but the two symptoms do not bear a constant relation to each other. There may be marked ataxy without great disturbance of equilibration, and, on the other hand, there may be great disturbance of equilibration without ataxy. There is, however, a tolerably constant relation between the disturbance of equilibration and the degree of impairment of sensibility, and the symptom is most marked in those cases in which the tactile sensibility is most deficient. The impairment or abolition of tactile sensibility is capable of being compensated for, up to a certain point at least, by the visual and other factors of the general consensus concerned in equilibration ; but when the eyes are shut, or the light withdrawn, equilibration becomes difficult or impossible. Even in perfectly normal individuals the tactile impressions require the aid of the visual, as evidenced by the greater or less degree of oscillation observable in most people when they try to stand with feet closely approximated and eyes shut.

The fact that equilibration is possible in the entire absence of the cerebral hemispheres, and therefore of sensation proper, indicates that this function is not necessarily correlated with consciousness or dependent on volitional effort. In the presence of the hemispheres, however, the same impressions which excite the adaptive activity of the mesencephalic and cerebellar centres also excite modifications of consciousness if attention

is directed to them. But the concentration of consciousness is in most cases rather a hindrance and source of confusion than an aid. The possible correlation of consciousness, however, complicates the question as to the independent action of the mesencephalic and cerebellar centres in cases of disease in man, and it is only by a consideration of the facts of experiment that we can exclude consciousness altogether as an essential factor. But while consciousness need not be excited in the normal exercise of the function, it is certain that abnormal conditions manifest themselves in consciousness in a painful manner in the form of vertigo or sense of insecurity; and to this in great measure are due the attempts to compensate for the derangement of an automatic self-adjusting mechanism by voluntary efforts at adaptation. These may succeed in overcoming a derangement which would render an animal deprived of its hemispheres utterly helpless.

The Influence of Visual Impressions.

§ 10. Equilibration and motor co-ordination may be acquired in the first instance and exercised without the aid of the eyes, as exemplified in those born blind. But in general, the acquisition of the motor adjustments necessary for maintaining equilibrium, and of all actions of any degree of complexity, is guided mainly by the sense of sight. The learner constantly keeps his eyes on his limbs, and his relations to surrounding objects, and *sees* that his movements are made in accordance with the end desired.

When the movements become organised and automatic by frequent repetition the guidance of the eyes ceases to be so necessary, and the impressions conditioned by the movements themselves are sufficient to ensure the requisite simultaneous and successive motor adjustments. But even then visual impressions, though not clearly affecting consciousness, are not inoperative, as is proved by the uncertain and wavering character of motor adjustments, even of the most habitual or automatic character, when the eyes are shut or the light withdrawn.

When there is defect or total default of tactile sensibility

equilibration is impossible except with the aid of vision. The sense of sight may compensate for a total absence of tactile (including muscular) sensibility, and an individual who has no sensibility in his lower extremities, and who falls like a log when he shuts his eyes, may stand or walk if he looks to his feet. This, however, always implies strained effort, and speedily induces fatigue. It would seem that the act of keeping the eyes open is of itself an aid to equilibration, though the eyes are useless as organs of vision. It has been observed[1] that ataxics, entirely blind, and able to stand with the eyes open, oscillate much more when they shut their eyes. This is probably due to the interruption of the act of fixed attention, of which the steady gaze, even with sightless orbs, is the physical expression.

The influence of vision on equilibration is further shown in the disturbances created by unusual movements in the field of vision; either by movements of the objects themselves or induced by faults in the oculo-motor apparatus. We associate our position in space not only with certain tactile sensations, but with a certain definite relation to surrounding objects. When the whole field of vision is in motion, or the positions of familiar objects are distorted by obliquity of the optic axes, there is a disturbance of the customary relations between the visual and tactile senses, and a distressing sense of insecurity results—the individual not being able to discriminate clearly whether he himself or the objects around him are in motion, or displaced. The difficulty of equilibration under such circumstances gives rise to the sense of vertigo, which is merely the subjective side of the physiological disturbance. Gazing intently at a running stream, or at some object like a railway train which completely fills the whole field of vision, causes in most people a sense of insecurity, and in many cases leads to actual overthrow of the equilibrium. Oscillation of the eyeballs or nystagmus, or the occurrence of paralysis in one of the ocular muscles, such as the external rectus, is a familiar cause of vertigo, which is attributed to what is termed 'erroneous projection,' or disharmony between the visual and tactile experiences and associations of our relations

[1] Erb, *Krankheiten des Rückenmarks*, Abtheil. 2, 1878, p. 94.

to surrounding objects. It has been found by Cyon[1] that pigeons are similarly affected by distortion of the optic axis. On placing prisms before their eyes he observed marked disorders of equilibrium, amounting in some to actual falling down. Sudden destruction of one eye in pigeons was found by Longet to cause the animals to spin round for a time on a vertical axis. This has been explained by Vulpian as an expression of a desire on the part of the animal to maintain its vision all round as usual, but it is probable that it may be a vertiginous movement consequent on the derangement of a bilateral visual association.

In all these cases of ocular vertigo the subjective element plays an important part, and it is difficult to determine how much, if any, disturbance of equilibrium would result from interference with the eyes or ocular muscles in the absence of true sensation, and apart from organised associations. The case is different, however, in respect to impressions originating in the labyrinth of the internal ear.

The Influence of Labyrinthine Impressions.

§ 11. The impressions which are generated in the semicircular canals of the internal ear form the most important factor in the afferent apparatus of the mechanism of equilibration, and the essentially reflex nature of the action is more clearly apparent.

The influence of the semicircular canals in this relation was first indicated by the experiments of Flourens[2] in 1828. These have been repeated and varied by many physiologists, and though some have questioned whether the phenomena observed are really connected with the semicircular canals as such, the arguments they adduce appear to me of little weight, and their explanations feeble and unsatisfactory.

The internal ear or labyrinth is embedded in the petrous portion of the temporal bone, and consists of a central chamber called the vestibule, which communicates in front with the cochlea and behind with the semicircular canals. On its

[1] *Op. cit.* p. 17.

[2] *Expériences sur les Canaux Semicirculaires de l'Oreille.*

outer aspect it opens towards the cavity of the tympanum, or drum of the ear.

The semicircular canals form three bony tubes, which open

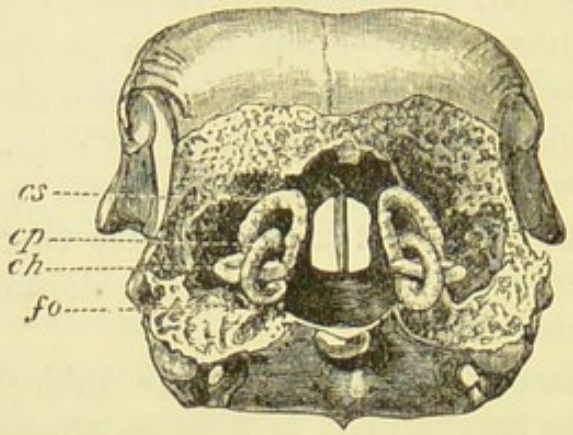


FIG. 47.—Semicircular Canals of the Turkey dissected out.—*ch*, horizontal canal. *cp*, posterior vertical canal. *cs*, superior vertical canal. *fo*, fenestra ovalis.

into the vestibule by five apertures, two of the tubes uniting into one (fig. 47).

The canals form each two-thirds of a circle, and at one end each presents a dilatation, or ampulla.

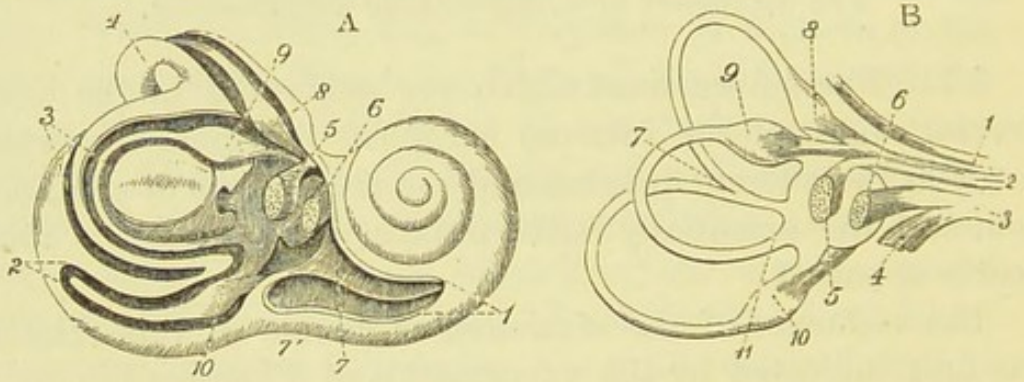


FIG. 48.—The Interior of the Right Labyrinth with its Membranous Canals and Nerves (Breschet).—A, the outer wall of the bony labyrinth is removed so as to display the membranous parts within. 1, commencement of the spiral tube of the cochlea. 2, posterior semicircular canal, partly opened. 3, external or horizontal canal. 4, superior canal. 5, utriculus. 6, sacculus. 7, lamina spiralis. 7′, scala tympani. 8, ampulla of the superior membranous canal. 9, ampulla of the horizontal. 10, ampulla of the posterior semicircular canal.—B, membranous labyrinth and nerves detached. 1, facial nerve in the internal auditory meatus. 2, anterior division of the auditory nerve, giving branches to 5. 8, and 9, the utricle and the ampullæ of the superior and horizontal canals. 3, posterior division of the auditory nerve, giving branches to the sacculus (6), and posterior ampulla (10), and cochlea (4). 7, united part of the superior and posterior canals. 11, posterior extremity of the horizontal canal.

The canals are termed respectively, according to their position and relation to each other, the superior vertical (fig. 47, *c s*; fig. 48, A 4); the posterior vertical (fig. 47, *c p*; fig. 48, A 2); and the horizontal (fig. 47, *c h*; fig. 48, A 3).

Within these bony tubes are membranous canals of the same shape as the bony canals (fig. 48) but of less diameter and separated from the osseous walls by a liquid termed the perilymph. Each canal has a dilatation or ampulla situated in the corresponding dilatation of the bony tube, and all communicate with a common sinus situated in the vestibule and termed the utricle (fig. 48, A 5). The membranous canals are filled with a liquid termed the endolymph. On the ampullary dilatations of the membranous canals are distributed respectively three branches of the vestibular division of the auditory nerve (fig. 48, B). The ultimate terminations of this nerve consist of fusiform cells furnished with hair-like processes, which project from the epithelial surface of the ampullæ. Embedded in the epithelial lining of the sinus and ampullæ are certain calcareous crystals, varying in form and size in different animals, termed otoliths or otoconia, which are intimately connected with the nerve terminations, and probably play an important part in their excitation.

The canals, being embedded in bone, and in close relation with a lobule of the cerebellum, are not easily isolated for purposes of experimentation, but in some animals the operation is easier than in others. An ingenious method has been adopted by Vulpian, viz. administering madder to the animals for some time previously, which causes the canals to become bright red in the midst of osseous tissue of a paler hue.

When the membranous canals are injured very remarkable disturbances of equilibrium ensue, which vary, as Flourens first pointed out, with the seat of lesion. This has been amply confirmed by the experiments of Cyon,[1] Spamer,[2] Högyes,[3] and others. According to the observations of Flourens and Cyon on pigeons, when the horizontal canal is divided on one side, the head is thrown into a series of oscillations in a horizontal plane round the vertical axis. These cease in a short time, but on section of the corresponding canal on the other side they reappear with greater intensity and the animal is unable to maintain its equilibrium, falling,

[1] Cyon, *Sur les Fonctions des Canaux Semicirculaires.* Thèse, Paris, 1878.
[2] Spamer, *Pflüger's Archiv*, Bd. xxi. 1880.
[3] Högyes, *Idem*, Bd. xxvi. 1881.

or turning on a vertical axis, or circling round and round. Flight is difficult or altogether impossible. After the lapse of eight to ten days, however, all the disturbances may have so subsided that except for some *maladresse*, especially visible in flight, the animal seems quite normal.

When the posterior vertical canals are divided the disturbances of equilibrium are of a similar character, but more violent. In this case the movements of the head are in a vertical plane, round a horizontal axis. Instead of spinning round a vertical axis, the animal tends to execute a somersault head over heels. These disturbances may all subside within a fortnight, leaving only a certain *brusquerie* in the movements and almost complete inability to fly.

Section of the posterior vertical canals causes movements of the head from behind forwards, and from right to left, or *vice versa*. There is profound disturbance of equilibration, and the animal tends constantly to turn somersaults heels over head. The plane of the movements of the head in this case is diagonally round a horizontal axis.

An analysis of the movements consequent on section of the respective canals shows that they take place in the plane of the canals operated on.

The effects of section of the semicircular canals in rabbits are of essentially the same character as those seen in pigeons. But they are more enduring, and in particular, as Cyon shows, the oscillations affect the eyeballs more than the head or trunk. When one of the horizontal canals is injured there is a tendency to movements of *manège*; when one of the vertical canals is injured the animal turns on its longitudinal axis. The eyeballs deviate and are thrown into a state of nystagmus, the plane of the oscillations varying with the canal injured. The oscillations of the eyeballs are more or less independent of movements of the head, and in fact are most pronounced when the head is fixed. The direction of the eyeballs will be the subject of future consideration (see p. 209).

In frogs also section of the semicircular canals causes very marked disorders of equilibrium, varying with the canals injured, the head turning on the longitudinal axis of the body, the animal falling to one side, on leaping, when the horizontal

canals are cut; falling on its back when the posterior vertical canals are cut; turning complete somersaults and exhibiting the utmost disorder of movement when the other vertical canals are divided. In a frog with the superior vertical canals divided, attempts at swimming are compared by Cyon to movements of waltzing in the water, the animal maintaining an upright position and pivoting round and round.

It has been observed that the disturbances of equilibrium after section of one or more of the canals, on one or both sides, are of comparatively short duration. When the whole of the semicircular canals on one side are destroyed the disturbances of equilibrium are also transitory. Equilibration is at first very uncertain, and flight is impossible. There is a tendency to fall towards the side injured, and in particular the leg of this side is observed frequently to give way suddenly as if it were broken. In many animals also the head assumes an unnatural position, the occiput being directed towards the side of injury, and the beak towards the opposite side. This condition has been specially described by Spamer,[1] and attributed by him to secondary implication of the cerebellum; but in a pigeon described by Munk,[2] in which the semicircular canals of the right side were deficient, the same distortion of the head was observed, apart from affection of the cerebellum or intracranial centres.

When the whole of the canals are destroyed on both sides the disturbances of equilibrium are of the most pronounced and almost indescribable character. Goltz [3] describes a pigeon so treated which always kept its head with the occiput touching the breast, the vertex directed downwards, with the right eye looking to the left, and the left looking to the right, the head being almost incessantly swung in this position in a pendulum-like manner. Cyon [4] says it is impossible to give an idea of the perpetual movements to which the animal is subject. It can neither stand, nor lie still, nor fly, nor maintain any fixed attitude. It executes violent somersaults now forwards, now backwards, rolls round and round, or springs in the air

[1] Högyes, *Pflüger's Archiv*, Bd. xxvi. 1881.
[2] Munk, *Du Bois-Reymond's Archiv*, 1878, p. 347.
[3] Goltz, *Pflüger's Archiv*, 1876.
[4] Cyon, *op. cit.*

and falls back to recommence anew. It is necessary to envelop the animals in some soft covering to prevent their dashing themselves to pieces by the violence of their movements, and even then not always with success.

The extreme agitation is manifest only during the first few days following the operation, and the animal may then be set free without danger, but it is still unable to stand or walk, and tumultuous movements come on from the slightest disturbance. But after the lapse of a fortnight it is able to maintain its upright position with some support, and to preserve any attitude given it, if not in any way disturbed, and gradually it begins to gain steadiness. At this stage it resembles an animal painfully learning to stand and walk. In this it relies mainly on its vision, and it is only necessary to cover the eyes with a hood to dispel all the fruits of this new education, and cause the reappearance of all the motor disorders.

It is only after the lapse of months that the animal again approaches a normal appearance. Even then its movements are all uncertain and insecure. Its march is slow, and it seems to be carefully feeling the ground. Flight is altogether impossible. By preference it remains in some obscure corner, as if anxious to avoid all disturbance or agitation. When it is suddenly startled it exhibits all the former confusion and tumbles about helplessly.

§ 12. Some physiologists (Böttcher,[1] Baginsky,[2] &c.) have endeavoured to explain away the phenomena observed after section of the semicircular canals on the assumption that the operations involve mechanical disturbance, or anatomical lesions in the cerebellar peduncles or other portions of the brain. But the experiments of Goltz, Cyon, Spamer, Högyes, and Laborde prove that the disturbances of equilibrium occur after methods of procedure which entirely exclude either mechanical or other lesion of the intracranial centres; and, apart from all other evidence, the undoubted fact that the disturbances vary with the canal injured completely disposes of such an hypothesis. Lesions of the cerebellum and neigh-

[1] *Archiv für Ohrenheilkunde*, Bd. ix. 1875.

[2] *Du Bois-Reymond's Archiv*, 1881, Heft 3 und 4.

bouring parts are apt to ensue some time subsequently to the operation, from secondary inflammatory changes set up by the wounds, but the symptoms which result from irritation or destruction of the semicircular canals in the first instance are entirely separate from such secondary complications. In what relation, then, do injuries of the semicircular canals stand to the disorders of equilibration observed ?

The first supposition which suggests itself is that the phenomena are related to disturbance of the sense of hearing, seeing that the lesions affect the mechanism of the ear. This, however, is not the case ; for Flourens and many other experimenters have shown that animals in which the semicircular canals alone have been destroyed retain their sense of hearing, so far at least as regards aërial vibrations. When the cochlea alone is destroyed animals lose their sense of hearing, but do not lose their faculty of equilibration. It has also been proved anatomically that the division of the auditory nerve which supplies the vestibule and ampullæ of the semicircular canals is a distinct branch from that which supplies the cochlea.[1] Whether the double origin of the auditory nerve corresponds to the two terminal subdivisions, as Cyon and Laborde assume, is not certainly established. The connection of the anterior root of the auditory nerve with the inferior peduncle of the cerebellum is probable, but the anatomical researches of Laura, and the experimental researches of Monakow[2] and Onufrowicz,[3] throw at least great doubt on the connection between this root and the so-called lateral nucleus of Clarke.

But it is an interesting fact that, as we descend the animal scale, the cochlea dwindles and disappears, while the semicircular canals remain well developed. The lamprey has only one saccule and two semicircular canals in its internal ear, and no external auditory meatus. Cyon found that though these animals gave no indications of hearing the loudest sounds, yet they exhibited the most profound disorders of equilibration when their semicircular canals were injured.

[1] This is so in all the lower animals, but Retzius states that in man the ampulla of the posterior canal is supplied by a division of the cochlear nerve.

[2] *Archiv für Psychiatrie*, Bd. xiv. Heft 1. 1883.

[3] *Ibid.* Bd. xvi. Heft 3.

They were unable to maintain their normal attitude, circled round and round when attempting to swim, or rotated round the axis of their bodies.

It is undoubtedly true that in the great majority of cases of Menière's disease, which is characterised by attacks of vertigo and disturbance of equilibrium, and which is dependent on disease of the internal ear, hearing is impaired. This, however, is easily accounted for on the supposition that the cochlea is also implicated in the disease. But we may have all the phenomena of Menière's disease without impairment of the sense of hearing, so far as relates to aërial vibrations. I have reported a case of this kind.[1] Results similar to those induced by injuries of the semicircular canals are caused by section of the auditory nerve itself. Goltz has shown that when the auditory nerve has been divided on both sides in the frog, the animal loses its power of maintaining its equilibrium when submitted to the balancing experiment already described. If its leg is irritated the animal jumps as before, but instead of alighting on its feet it falls on its back, or in some other irregular fashion, and rolls over and over before it can regain its normal position.

More recently Bechterew[2] has described similar effects of section of the auditory nerve in dogs. The animals roll round towards the side of operation, and exhibit a skew deviation of the eyes—that on the side of section looking downwards and outwards, the other upwards and inwards, and oscillating in the opposite direction. The rolling is most marked during the first few days after the operation, being then almost incessant. When not rolling on its axis the animal lies on the side of section, with this side of the head downwards, the other upwards. The legs on the side of section are doubled up close to the trunk, but flaccid, while those on the opposite are rigidly extended outwards. If the animal, however, is placed in any other position than on its side, all the stiffness of the limbs ceases to be manifest. The disturbances of equilibrium gradually become less pronounced; but for many weeks after the operation the animal is very unsteady. This

[1] 'Labyrinthine Vertigo,' *West Riding Asylum Reports*, vol. v. 1875.

[2] *Pflüger's Archiv f. Physiologie*, Bd. xxx. 1883.

is greatly increased by covering the eyes, and a loud sound frequently causes the animal to fall on its side—the side of section—or roll round once or twice.

When both auditory nerves are cut the animal can neither stand nor walk. There is no paralysis of the limbs whatever, but all the movements are irregular and purposeless. The head and eyes oscillate, but the eyes oscillate in a horizontal plane, and there is no skew deviation as when only one nerve is divided.

These results might be ascribed to injury of some part of the brain in the attempt to divide the auditory nerve within the skull, but both Goltz and Bechterew give satisfactory evidence against this view. Goltz has shown that when that portion of the skull of the frog which contains the internal ear is detached from the rest, without opening the intracranial cavity, the results are still the same, thereby excluding the possibility of intracranial lesion.

§ 13. The disturbances are attributed by some (Vulpian, Brown-Séquard, &c.) to reflex motor reaction, excited by the irritation consequent on the operative procedure. But, though this may explain some of the first effects of the lesions, it is evidently not all; for, as Goltz observes, the phenomena continue long after the wounds have entirely healed up. Nor are they explicable on the supposition of an auditory vertigo, or psychical confusion, occasioned by a disharmony between conscious impressions and ideas; for it has been shown by Flourens, Lowenberg, and Bechterew that the disorders occur in animals in which the cerebral hemispheres have been removed or functionally annihilated. But that psychical confusion does play some part in the disorders is evident from the fact that they are more marked, and come on spontaneously in animals retaining their hemispheres, while some external stimulation is necessary to excite them after destruction of the hemispheres. But this psychical confusion and panic are only the subjective side of the disturbance of a mechanism which is essentially reflex in character. The intensification of the disturbances by the emotions of fear and dread is merely an illustration of a fact familiar in human experience under similar circumstances.

There can, I think, be no room for doubt that the disturbances of equilibrium above described are in direct causal relationship with the lesions of the semicircular canals or auditory nerves as such, apart from all mechanical or organic lesion of the intracranial centres. But there is room for discussion as to whether the disturbances are due to irritation or destruction of the nerves, or their peripheral expansions in the labyrinth—a point which I reserve for consideration in a subsequent chapter (see Chapter VI. § 19).

But, whether we attribute them to irritation or destruction, or both, the phenomena observed in connection with lesions of the semicircular canals clearly point to these organs as the source of impressions which are necessary for the maintenance of the equilibrium, and without which optic and tactile impressions alone barely suffice even after prolonged education.

The hypothesis, originated by Goltz, that the semicircular canals constitute an afferent apparatus for the maintenance of the equilibrium of the head, and with it of the body in general, is perhaps too narrow; for, as has been seen, movements of the eyeballs, and also of the trunk and limbs, are in relation with the canals as well as movements of the head. As Cyon observes, the head is affected specially only in pigeons; whereas in frogs it is the trunk, and in rabbits the eyeballs; to which may be added, that in dogs, according to Bechterew's experiments, head, eyes, trunk, and limbs are all involved. These facts indicate, therefore, that the semicircular canals are in relation with all the movements which are concerned in equilibration in different animals.

§ 14. The exact mode of origination of the labyrinthine impressions has been much discussed, and it would be premature to say that the point is definitively determined. The hypothesis advanced by Goltz, and supported in all essential points by the investigations of Mach,[1] Breuer,[2] and Crum-Brown,[3] is that the impressions are conditioned by the degree, and relative variations, of pressure exerted by the endolymph upon the ampullary dilatations of the membranous canals on which the

[1] *Sitzungsberich. d. Wien. Acad.*, Bd. lxviii. 1873.
[2] *Wien. Med. Jahrbücher*, 1874 and 1875.
[3] *Journal of Anatomy and Physiology*, vol. viii. 1874.

vestibular nerves are spread. This hypothesis has, however, been contested by Cyon and others, on the ground that variations in pressure in the canals, experimentally induced, do not cause disturbances of equilibrium. Cyon's hypothesis is that vibrations of the otoliths, conditioned by movements of the head and undulations of the endolymph, are the immediate excitants of the ampullary nerves.[1] But, whether it is tension or otolithic vibration, we may assume, with Goltz, that each variation in the position of the head will excite irritation of the ampullary nerves according to the plane in which the movement takes place. If it is pressure, inclination of the head to the right side will cause the endolymph to flow *from* the right ampulla and *to* the left, and *vice versa* if the head is inclined to the left. These symmetrical *plus* and *minus* variations may be supposed to excite the centres of equilibration to action appropriate to the position of the head and body associated therewith. When the conditions are perverted, by lesions of the canals, disturbances of equilibrium are the necessary result; and these will vary according to the seat of lesion.

§ 15. It is by means of the semicircular canals that we are aware, according to Crum-Brown, of the axis, rate, and direction of rotation of the head and body, apart from all other channels of perception. If a person be placed on a revolving disc, with his eyes shut, he is still able to determine the sense and extent of the angle through which his body has been revolved.

When rotation has been kept up for some time the rate gradually appears to diminish, and after a longer time all sense of rotation entirely disappears. When the rotation is stopped the individual feels as if he were being whirled round

[1] Sewall (*Journal of Physiology*, Feb. 1884, vol. iv. No. 6) finds that in sharks and skates destruction of the semicircular canals is often entirely negative as regards disturbances of equilibrium. When disorders of equilibrium did occur they were more particularly observed in connection with injuries of the vestibular sacs, particularly the saccules, rather than of the ampullæ. Laceration of the saccules and removal of the otoliths seem to have been most effective in inducing disturbances. During this process nystagmus was always very marked, and frequently vomiting occurred even when equilibrium was not affected afterwards.

in the opposite direction. If at this period he opens his eyes a distressing sense of vertigo comes on, explicable by the discord between his visual, tactile, and labyrinthine impressions. The hypothesis is that rotation in a plane perpendicular to any of the canals causes the endolymph, on account of its inertia, to press in the reverse direction against the ampullary nerves. This gradually ceases as the movements of the liquid and bony canals become equalised, and so the rotation ceases to be felt. On stoppage of the rotation, however, the endolymph continues to move on, and an impression of rotation in the reverse direction is occasioned. This also ceases after a time, owing to friction, and the phenomena subside. 'Each canal,' as Crum-Brown argues, 'has an ampulla at one end only, and there is thus a physical difference between rotation with the ampulla first and rotation with the ampulla last; and we can easily suppose the action to be such that only one of these rotations (say with the ampulla first, in which case, of course, there is a flow from the ampulla into the canal) will affect the nerve termination at all. One canal can, therefore, on this supposition, be affected by and transmit the sensation of rotation *about one axis in one direction only*, and for complete perception of rotation in any direction about any axis *six* semicircular canals are required, in three pairs, each pair having its two canals parallel (or in the same plane), and with their ampullæ turned opposite ways. Each pair would thus be sensitive to any rotation about a line at right angles to its plane or planes, the one canal being influenced by rotation in the one direction, the other by rotation in the opposite direction.' These conditions are fulfilled by the fact that the two horizontal canals are on the same plane, and the superior vertical canal on the one side is in the same plane as the posterior vertical canal on the other, and *vice versa* (see fig. 47). Thus in each case there is one canal—the horizontal—at right angles to the mesial plane, and two other canals—the superior and posterior vertical—equally inclined to the mesial plane. Though, as has been stated, there are some difficulties in the way of accepting the hypothesis of variations in tension, yet that the ampullary nerves receive stimulation respectively under such conditions as described by Crum-Brown, Mach, and

Breuer is in the highest degree probable; and we can thus furnish an explanation of facts otherwise inexplicable.

Important confirmation of these views is afforded both by experiments on animals and also on deaf mutes, especially those who have become so from disease. Breuer [1] affirms that vertigo cannot be induced by rotation in pigeons whose semicircular canals have been destroyed; and Högyes [2] states that the same is true of rabbits whose membranous canals have been extracted. James [3] found that a large proportion of deaf mutes (186 in 519) were totally insusceptible of being made dizzy by rapid rotation; while in two hundred normal individuals only one remained exempt. In a note appended to the memoir one observer reports that out of twenty cases, half of whom had been born deaf, and the other half had lost their hearing from disease, the latter could not be made dizzy by rotation, whereas in the former a few seconds' spinning were sufficient to excite vertigo.

It is no valid argument against the functions ascribed to the semicircular canals to assert that, as the disturbances are only temporary, therefore the phenomena are due purely to reflex irritation. If the semicircular canals were stated to be the *only* afferent organs of equilibration the argument would have weight; but the organs themselves are double, and in their entire absence compensation is possible through the agency of visual and tactile impressions. The fact that closure of the eyes intensifies the disorders, and renews them when they have almost ceased, shows how much the recovery is dependent on the functional compensation effected by the other factors of the afferent consensus.

II. Co-ordination of Locomotion.

§ 16. Animals deprived of their cerebral hemispheres, besides being able to maintain their equilibrium, are also capable of locomotion in their usual manner. Fishes balance themselves with their fins, and by alternate lateral strokes of the

[1] *Op. cit.* [2] *Op. cit.*

[3] 'The Sense of Dizziness in Deaf Mutes,' *American Journal of Otology*, Oct. 1882.

tail swim forward with the same precision as before; frogs leap on land, or swim when thrown into the water; birds, if urged, walk forward, or fly if thrown into the air; rabbits bound away in their characteristic mode of progression, in response to appropriate external stimuli.

For reasons above stated it is impossible, in the higher animals, to demonstrate, experimentally, the retention of the faculty of co-ordinated locomotion in the centres situated below the hemispheres, but we are able to arrive at the same conclusion in another way. It is a fact of every-day observation that the function of locomotion, once set in action, is carried on with all regularity and precision, without attention and apparently without consciousness, while the cerebral hemispheres are practically detached and engaged in other directions. From the homology subsisting between the mesencephalic and cerebellar centres of man and the lower vertebrates we argue the homology of function, and what we have seen to be true of the lower animals is to be regarded as more or less true of man. It may be, but we have no means of determining with exactitude, that this function is, in the lower animals, primarily or hereditarily inherent in the constitution of their nerve centres, and that in the higher it is rather, as Carpenter expresses it, a secondary reflex or automatic action, i.e. the result of previous experience and conscious action. Whichever way we look at it, the result is the same, viz. that, whether primarily or secondarily developed, the co-ordination of movements of locomotion is a function of the lower centres.

It is manifestly impossible to draw a hard and fast line between the functions of equilibration and of locomotor co-ordination, for without equilibration locomotion becomes impracticable, and the same afferent factors are concerned in both. In discussing the function of equilibration I have frequently spoken of the two together; but, theoretically, the two functions are capable of differentiation from each other. We can conceive an animal possessed of the power of maintaining its bodily equilibrium, and of the necessary muscular adjustments to this end *in loco*, but unable to move out of its position. Therefore, even though we may not be able to

separate them practically, or localise the two functions in clearly differentiated centres, it is convenient to consider them apart.

The mechanism of co-ordinated locomotion, like the mechanism of equilibration, consists of—1, an afferent system; 2, a co-ordinating centre; 3, an efferent or motor system, by which the centre is brought into relation with the muscles of the trunk and limbs.

That which excites the centre to action, in the first instance, may be various. In the animal deprived of its hemispheres it can only come from without, and is generally some form of tactile stimulus.

The central apparatus of locomotion, once set into activity, continues to functionate (to use a convenient expression) in a rhythmical manner. The duration of this activity coincides with the degree of intensity or continuance of the primary stimulus, and the vitality of the nervo-muscular apparatus. The fish in the water is under continual stimulation of its body surface by contact with the mobile water, and, therefore, it continues to swim till arrested by some obstacle or by fatigue. The rhythmical strokes of the tail would appear to be in a great measure conditioned by each other, the one stroke exciting the opposing stroke in regular succession. So the frog, when thrown into the water, is impelled to swim by the same kind of stimulus which acts on the body of the fish. The leaping movements on land are kept up in rhythmical succession by the successive impressions of contact with the ground after each leap. The pigeon makes bilateral rhythmical movements of the wings; quadrupeds either leap or walk, in the latter case usually with diagonally co-ordinated action of the fore and hind limbs; while man progresses principally by alternate pendulum-like swings of the lower extremities—the rhythmical succession being kept up by the alternate impressions of contact with the ground, which the sole of the foot receives after each step. Though in man the upper extremities have become differentiated away from purely locomotive purposes, yet it may be observed that they are co-ordinated with the lower extremities in the same diagonal manner as in quadrupeds; the right hand swinging with the left leg, and *vice versa*. The

upper extremities are likewise co-ordinated with the other bodily movements, in the adjustments necessary to the maintenance of equilibrium.

§ 17. Locomotion involves a vast complexity of motor adjustments of the head, trunk, and limbs beyond the simple synergic combinations of the muscles of the limbs which are co-ordinated in the spinal cord, and are capable of being called forth by stimulation of the anterior roots (see Chapter II. § 17). The centre of gravity is continually varying, and each movement of the active limbs necessitates graduated adjustment of the trunk and apparently passive limbs, in order that the movements *d'ensemb'e* may be carried out in even simultaneity and succession without abruptness, and in harmonious relation with each other. By stimulation of the cord below the calamus scriptorius, the limbs of rabbits, as Ludwig and Woroschiloff have shown, may be thrown into co-ordinated and alternating action such as are seen in running and leaping; and similar co-ordinated actions of the limbs may be called forth reflexly in animals deprived of all centres above the spinal cord. But the spinal centres alone are unable to provide for the execution of these movements in relation to the body as a whole, and its surroundings, which are implied in locomotion from place to place. These necessitate the presence and activity also of the mesencephalic and cerebellar centres.

During the acquisition of all movements of any degree of complexity, not already organised, or, if so, insufficiently developed, the learner directs his movements in large measure by the aid of vision, and plants his body and limbs in the position he sees best adapted for carrying out the end desired; and he is guided also, and the energy of his motor adjustments regulated and graduated, by the sensations and impressions arising in connection with muscular action. When facility has been acquired, neither vision nor the sense of muscular action seems necessary, and the most complex co-ordinations can be effected with the utmost precision without attention, and even without consciousness. What was at one time a conscious effort becomes an organised reflex, provided for in the mechanism of the lower nerve centres; and it is only under certain abnormal conditions that the conscious factors,

formerly at work, again assume importance. This is exemplified, and the conditions necessary to locomotor co-ordination illustrated, in tabes dorsalis, or locomotor ataxy. In this affection, which is due to disease of the posterior columns of the spinal cord, there is a remarkable combination of disorders of station and locomotion. The individual so affected stands with difficulty, and totters and stumbles in his gait, and the movements of his limbs are characterised by an excessive energy, *brusquerie*, and irregularity, altogether striking and pathognomonic. The disorderly energy and uncertainty are manifested mainly in the lower extremities, but they may occur also in the upper extremities, and in some cases also in the muscles of articulation. All the disorders of the limbs are intensified when the eyes are shut or the patient is in the dark. In the recumbent posture he can move his limbs freely in all directions and with energy; and in this position can co-ordinate his limbs for volitional purposes without appreciable unsteadiness, even when his gait is already profoundly ataxic. Mention has already (p. 124) been made of the difficulty of maintaining the balance; a symptom which is most marked in those cases in which there is impaired sensibility in the soles of the feet. So long as the eyes are open the patient is able to maintain his equilibrium, but in the dark, and when the eyes are shut, he oscillates greatly, and is in danger of falling if unsupported. In the great majority of ataxics tactile sensibility is perverted. The individual suffers from severe lancinating pains, there is numbness of the feet, retardation of sensation, and various other indications of sensory impairment. There is want of tone in the muscles, and the so-called tendon reflexes are abolished.

§ 18. There is considerable diversity of opinion as to the explanation of the disorders characteristic of ataxy. Some (Erb, &c.), who hold that the spinal cord itself is not a centre of co-ordination attribute the symptoms to disease of hypothetical centrifugal co-ordinating tracts. But we have already seen that synergic co-ordination is a function of the spinal centres themselves; and we have no reason for assuming that there exist centrifugal tracts other than those of the anterior

and lateral columns, which call into play the spinal centres. The morbid anatomy of the disease shows beyond all doubt that all the symptoms characteristic of ataxy may be manifested in the entire absence of any abnormality in the antero-lateral tracts and anterior roots. The disease affects tracts which are essentially centripetal, as shown by the direction of secondary degeneration. But, though centripetal, they are not the paths of sensation proper, except in so far as that the posterior roots run for a certain distance in the posterior root zones before entering the grey matter and reaching the opposite side of the cord. Though in a large proportion of cases there is impairment of tactile and general sensibility, yet in others, in which ataxy has existed in a marked degree, this has not been found; and there appears to be no constant relation between the degree of ataxy and the extent of impairment of tactile, muscular, or general sensibility. There may be the most profound anæsthesia without ataxy. This is the case in anæsthesia of cerebral origin, in which the centres or tracts of sensory perception are destroyed. And there is a remarkable case on record [1] of total anæsthesia of spinal origin in which there was complete retention of motor power without ataxy. The patient had no sense of his limbs or of the energy of his movements; but, though he could not stand with his eyes shut, yet with his eyes open he could walk and co-ordinate all his movements with fair precision, and without any of the abruptness and irregularity seen in ataxy. Even with his eyes shut he could will and carry out a desired movement without any greater uncertainty or vacillation than characterises the actions of perfectly normal individuals under similar conditions. This case proves beyond doubt that sensation, cutaneous or muscular, is not indispensable to motor co-ordination. However necessary it may be as a guide to the acquisition of complex movements in the first instance, the power, once acquired, can be exercised without the aid of any sense of movement actually effected. But, though there may be total anæsthesia without ataxy, it is quite possible, as has been insisted on by Leyden,[2] that there

[1] Schüppel, *Archiv d. Heilkunde*, Bd. xv. 1874.

[2] Tabes Dorsualis, art. Eulenburg's *Real-Encyclopädie*, 1883.

may be disorders of sensibility in ataxics, not readily determined by ordinary methods of examination, which exercise a *positive* disturbing influence, and lead to false judgments as to the energy and graduation of the various motor adjustments. In ataxy sensation is more frequently perverted, and the rate of transmission retarded, than actually abolished. The positive disturbing influence of such conditions cannot be considered as disproved by the occurrence of a total anæsthesia without ataxy; but it is not necessary that we should assume that they are invariably present. There is reason for believing that ataxy may exist apart from false sensations, or erroneous judgments founded on them. I am not aware that any case has been actually reported, but the probability is that in sclerosis of the posterior columns, conjoined with cerebral hemianæsthesia, ataxy would be just as pronounced on the one side as the other; though, from the nature of the lesion, any disturbances of sensation proper would be entirely eliminated.

As the posterior root zones—disease of which is the essential cause of ataxy (Charcot and Pierret)—belong to the fundamental spinal system, and vary with the development of the spinal segments, it is probable that they contain fibres which, independently of sensation, and in a purely reflex manner, serve to secure, in harmonious and graduated relation to each other, the synergic combinations organised in the spinal centres, the stimulus to each being supplied by the activity of that with which it is immediately associated. The more complex the combinations, the greater the necessity of such a system of fibres. Hence locomotion, which involves the graduated activity of so many centres, is more likely to suffer than the more simple synergic combinations of the muscles concerned in any individual movement of the limb, when the posterior root zones are invaded by disease. Simple acts of volition might still be carried out with a fair amount of precision when locomotion would be difficult or altogether impossible. Such is the condition actually seen in ataxy, and it is only in the extreme stages, when the lesions are more diffuse, that co-ordination in general has the same abrupt and tumultuous character as that of locomotion. With the aid of

vision an ataxic is able to overcome to a large extent the uncertainty and irregularity of his movements, which otherwise would be very evident; but this involves considerable strain, and his efforts to compensate by volitional action for the defects of a self-adjusting mechanism speedily induce exhaustion and fatigue. So long also as sensation is not seriously impaired, the sense of muscular action enables him, to some extent, to guide his movements and graduate his motor innervation irrespective of vision, and in some degree to repress the disorderly tendency of his limbs.

But no conscious efforts can ever entirely make up for the defects of the self-adjusting mechanism of motor co-ordination; and, from the complete retention of all motor co-ordination in animals deprived of their cerebral hemispheres, we may conclude that this is provided for and organised in the centres situated below those of consciousness and volition.

III. Instinctive or Emotional Expression.

§ 19. Animals deprived of their cerebral hemispheres are still capable of exhibiting, in response to various forms of sensory stimulation special and general, reactions, more or less complex, which do not at all differ in character from those which we associate with feeling or emotion. They start at sounds, flinch at light thrown in their eyes, or even direct their movements in relation with retinal impressions; respond by movements expressive of disgust or discomfort at unpleasant nasal or gustatory stimuli, and make the most varied reactions to stimulation of the nerves of common sensation. Frogs croak, as if from pleasure, when their backs are gently stroked; and rabbits scream piteously, and exhibit the various signs of agitation characteristic of intense pain, if their toes are pinched, or any sensory nerve severely stimulated. The outward manifestation of feeling is a purely instinctive or reflex act, over which we have little or no control, and which we can simulate only so far as those movements are concerned which are also under volitional control. But the changes in the pupils, the affections of the secretions, of the rhythm of the heart, and the visceral concomitants of feeling are beyond

our control, and manifest themselves only in relation with the actual existence of the exciting cause, and in spite of all attempts to suppress them.

But the physical embodiment, or outward expression of feeling, does not necessarily imply the existence of pain or feeling as a state of consciousness. As all the physical manifestations of feeling are capable of being called forth in animals deprived of their cerebral hemispheres, which alone are the substrata of consciousness, we must regard them as merely the reflex or instinctive response of centres in which sensory impressions are correlated with the motor, vasomotor, and secretory apparatus.

The phenomena observed in animals deprived of their cerebral hemispheres are in all respects analogous to those observed in human beings under the influence of chloroform. Chloroform, as proved by actual experiment, first annihilates the excitability of the hemispheres—a condition coinciding with the abolition of consciousness—but the mesencephalic and lower centres retain their excitability long after this point has been reached. Hence impressions which under normal conditions would excite pain, as well as groans, cries, and the other physical expressions of pain, merely excite the physical manifestations without any painful sensation proper. These are no more expressive of conscious suffering than the notes elicited by striking the keys of a pianoforte are indicative of pleasure or pain on the part of the instrument (Crichton-Browne).

The centres of emotional expression are therefore situated below the centres of conscious activity and ideation, and must necessarily be in relation with every form of centripetal and centrifugal impulse through which signs of feeling may be induced or manifested. These conditions are not furnished below the mesencephalic centres. With these, however, as the experiments of Vulpian and others have shown, every form of reaction, excepting perhaps the reactions special to the olfactory nerve, may be elicited in response to appropriate peripheral stimulation, in all respects like those of the unmutilated animal.

But, though the facts above related prove that in the absence of the cerebral hemispheres acts of extraordinary

complexity—equlibration, co-ordinated locomotion, adaptive reactions, and signs of feeling in response to sensory stimulation—are capable of being carried out, it is a problem of surpassing difficulty to analyse the mechanism of the various manifestations, and specialise the centres in which they are individually localised.

In the following chapters an attempt will be made to determine the functions of the different centres; though, at the outset, I would remark that the cerebellar, mesencephalic, and spinal centres cannot possibly be detached or considered apart from each other.

CHAPTER V.

FUNCTIONS OF THE OPTIC LOBES OR CORPORA QUADRIGEMINA.

§ 1. The optic lobes, or corpora bigemina of fishes (fig. 44, B), batrachians (fig. 43, B), and birds (fig. 45, B) are structurally homologous with the corpora quadrigemina of mammals. The general anatomical relations of these ganglia have already been mentioned (Chapter I. § 8). They were seen to be connected with the reticular formation and antero-lateral tracts of the spinal cord through the upper and lower fillet on the one hand, and with the corpora geniculata, optic tracts, and cerebral hemispheres on the other. In the ventral and ventro-lateral aspect of the central grey substance of the aqueduct of Sylvius the nuclei of the third, fourth, and portion of the fifth cranial nerves were seen to be situated (fig. 19). The superficial origin of the optic tracts from the optic lobes is at once apparent in the lower vertebrates, and from the anterior tubercles or nates in many mammals, such as the rabbit. The connection is less direct in monkeys and man, but on careful exposure of the parts it is clearly evident that the anterior brachium is continuous with the optic tract through the corpus geniculatum laterale (fig. 18, *c g e*).

The testes, or posterior tubercles, seem to have no direct relation with the optic tracts in the lower mammals. In the monkey and man their arms, or brachia, pass into the corpora geniculata media (fig. 18, *c g i*). From these tubercles are traceable certain portions of the optic tracts, which, however, form a commissure in the chiasma (the inferior commissure), and do not appear to enter into the composition of the optic nerves (Gudden).

The testes consist of a superficial stratum of fibres, constituting the origin of the posterior brachia, and a lenticular

mass of grey matter, consisting mostly of small multipolar nerve cells, into which radiate fibres of the brachia from the surface, and also fibres from the lower fillet, which, partially at least, decussate with those of their fellows on the opposite side. Meynert regards the brachium of one side as directly related to the fillet of the opposite side; but it is more probable that the relations between the brachia and the fibres of the fillet are only indirectly established through the grey matter. The valve of Vieussens connects the upper vermiform process of the cerebellum with the testes.

The anterior tubercles or nates have a greyer tint than the testes, and have on the surface a superficial or zonal stratum of fibres continuous with the anterior brachia or optic tracts.

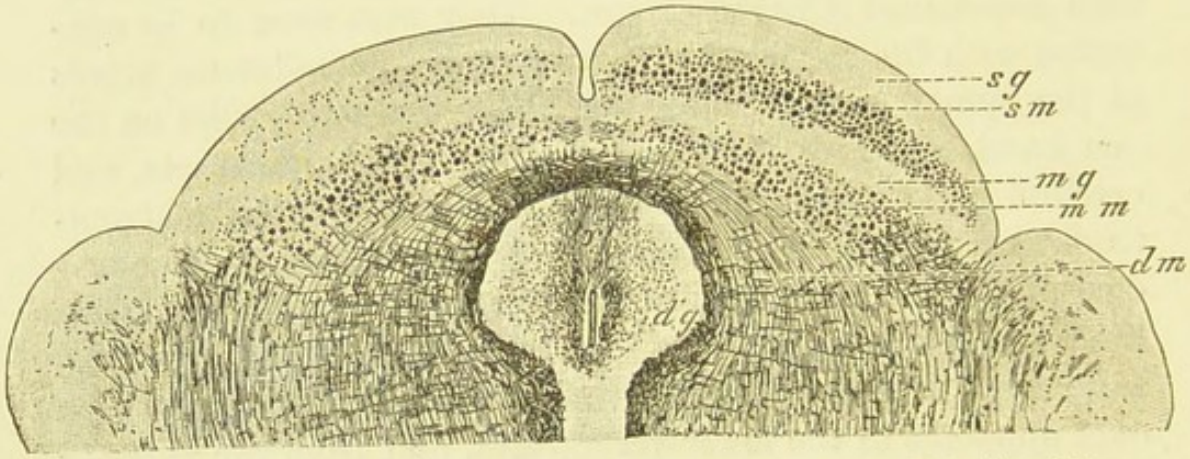


FIG. 49.—Frontal Section of the Nates (Corpora Quadrigemina) of the Rat. The right eye had been enucleated. × 12. (After Ganser.) *s g*, superficial grey matter. *s m*, superficial medullary layer. *m g*, middle grey layer. *m m*. middle medullary layer. *d m*, deep medullary layer. *d g*, deep grey layer. *x*, radial fibres, probably connected with the oculo-motor nuclei.

This is succeeded by a layer of finely granular grey matter (fig. 49, *s g*) interspersed with numerous small multipolar cells. In birds the granules of this layer are disposed in beautifully concentric lines parallel with the surface of the optic lobes. Underneath the superficial grey or granular layer is a stratum of greyish-white appearance (Tartuferi's [1] strato bianco-cinereo superficiale), in which may be differentiated a layer of fibres (fig. 49, *s m*) which pass directly into the optic tracts; and also according to the researches of Ganser [1] and Monakow,[2] a

[1] *Sull' Anat. Minut. dell' Eminenze Bigem. Ant. delle Scimie, Rivista Sperimentale*, 1879.

deeper grey layer (fig. 49, *m g*) containing nerve cells of different sizes, and a layer of fibres (fig. 49, *m m*) which connect the nates with the optic radiations and visual centres of the cerebral hemispheres.

More internally, and immediately surrounding the central grey substance (fig. 49, *d g*) are fibres derived from the upper fillet (fig. 49, *d m*) which decussate with each other above the aqueduct of Sylvius, and send radiating fibres into the overlying structures. Other radial fibres exist which pass from the superficial layers inwards through the central grey substance, and, according to Meynert, connect the proper optic centres of the corpora quadrigemina with the oculo-motor nuclei (fig. 49, *x*).

§ 2. The obvious anatomical connection between the optic tracts and the anterior quadrigeminal tubercles of mammals is sufficient to indicate that these centres have some important relations to retinal impressions. But it would not follow that they are visual centres proper, even though destructive lesions should cause blindness. For such lesions would necessarily break the continuity of the optic tracts in their more or less direct path to the true centres of vision in the cerebral hemispheres.

The facts of anatomy, however, as well as those of physiological and pathological experiment, indicate that the corpora quadrigemina, though not the centres of vision proper, are centres of co-ordination between retinal impressions and motor reactions or adjustments of considerable complexity. It is, however, excessively difficult, if at all possible, to differentiate clearly between the effects of lesions of the quadrigeminal lamellæ proper and those of the tracts with which they are related. Until these are more definitely determined we may include among lesions of the corpora quadrigemina not merely lesions of the lamellæ above the aqueduct of Sylvius, but also of the subjacent tracts and nuclei of the tegmentum.

When the hemispheres are removed the pupils still con-

[1] 'Die periph. u. cent. Anordnung d. Sehnervenpaare u. d. Corpus Bigem. Ant.,' *Archiv f. Psychiatrie*, Bd. xiii. 1882.

[2] 'Die Bezieh. d. sogenannt. Sehsphäre z. d. infracorticalen Opticuscentren u. z. n. Opticus,' *Archiv f. Psychiatrie*, Bd. xiv. 1883.

tract to light, and the eyes are moved in response to retinal impressions and in accordance with variations in the position of the head and body. The conditions of irido- and general oculo-motor action are furnished by the nuclei of the third and fourth nerves in the ventral aspect of the aqueduct of Sylvius and the nuclei of the sixth nerves in the medulla oblongata, connected with each other through the posterior longitudinal bundles. The nuclei of the sixth nerves co-ordinate the external lateral movements of the one eye with the internal movements of the other (p. 28). The researches of Hensen and Volckers[1] have shown that the nuclei of origin of the third nerve contain separate centres for the individual oculo-motor actions. After removal of the cerebral hemispheres in dogs they found that the application of electrical stimulation to the floor of the aqueduct of Sylvius, and posterior part of the third ventricle, gave rise to different ocular movements, according to the position of the electrodes.

Most anteriorly, in the wall of the third ventricle, is the centre for accommodation (fig. 50, *A c c*), acting on the tensor of the choroid through the anterior root fibres of the third nerve. Behind this is the centre for the constrictor fibres of the iris (fig. 50, *J r*).

Next, at the point of junction of the third ventricle with the aqueduct of Sylvius, is the centre for the rectus internus (fig. 50, *Rect. int.*), and further in order backwards, centres for the rectus superior, levator palpebræ superioris, rectus inferior, and lastly that of the trochlearis or obliquus superior, the centre of which lies below the testes and somewhat laterally (fig. 50, *R u O*).

From these anatomical and physiological data it would be natural to conclude that the optic lobes are the centres of correlation between retinal impressions and oculo-motor reactions. Section of the one optic nerve causes paralysis of the reflex contraction of the pupil to light on that side. But, owing to the commissural relations between the oculo-motor nuclei, light thrown into the sound eye excites contraction of the pupil on both sides, though more speedily and more vigorously on the sound side.

[1] *Archiv f. Ophthalmologie*, Bd. xxiv. 1878.

§ 3. Flourens found that destruction of the optic lobes in birds caused blindness and dilatation of the pupils, with cessation of their reactions to light; and that the relations of the eyes to the optic lobes were entirely crossed—destruction of the left lobe causing total loss of vision in the right eye, and *vice versa*. The cross relations between the eyes and optic lobes have their foundation in the decussation of the optic tracts in the optic chiasma, but the extent of this decussation varies in different animals. In fishes the decussation is a complete

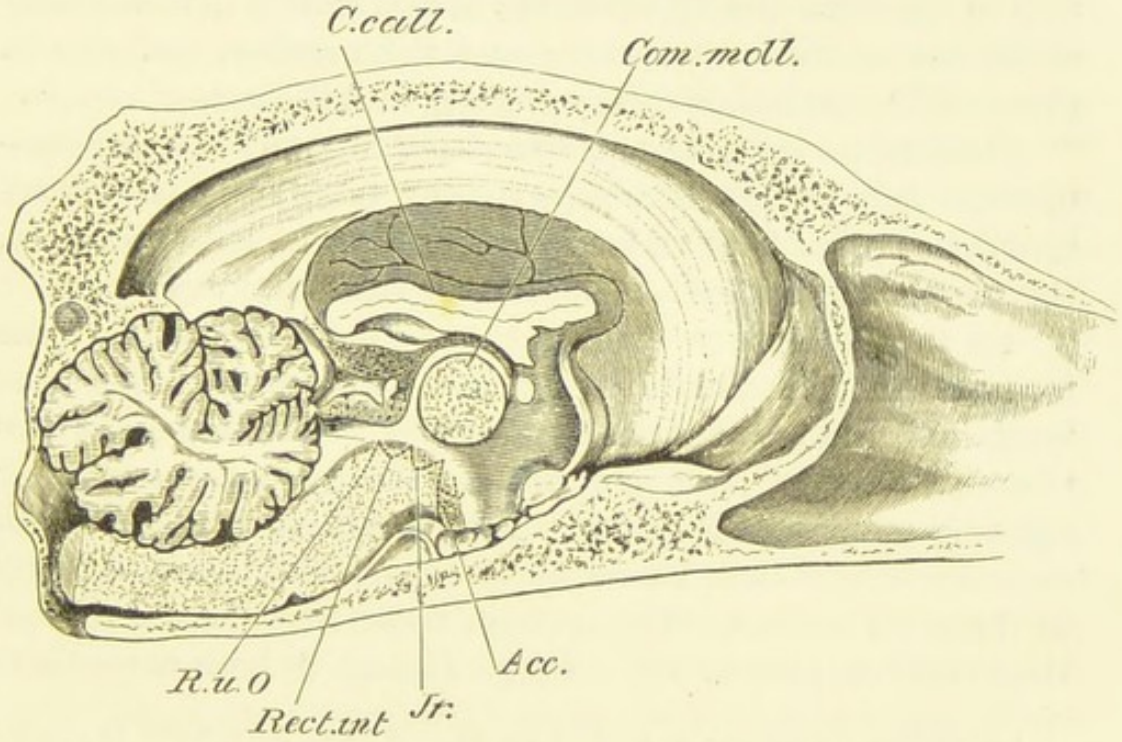


FIG. 50.—Sagittal Section of the Skull and Encephalon of the Dog. (Hensen and Volkers.) *C. call.*, corpus callosum. *Com. moll.*, commissure mollis. *Acc.*, centre of accommodation. *Jr.*, centre for the sphincter iridis. *Rect. int.*, centre for the rectus internus. *R.u.O*, centres for the rest of the ocular muscles.

one, and is in some at once apparent, as the one nerve merely passes below the other. In frogs and birds the tracts decussate through each other, but in them also the decussation is generally regarded as a complete one. When one optic lobe is destroyed in a frog or a bird blindness ensues only in the opposite eye, and its optic tract and retina undergo degeneration.

In the case of mammals considerable differences exist, depending probably, as Gudden has suggested, on the degree

of separation of the fields of vision. Those mammals[1] whose fields of vision are entirely separated, such as the horse, the ox, sheep, &c., have entire decussation of the optic tracts; while those in which the two fields of vision fall together more or less have a correspondingly partial decussation of the optic tracts in the chiasma.

Though it has been contended, mainly on the ground of anatomical and histological examination, by Besiadecki,[2] Mandelstamm,[3] Michel,[4] Schwalbe,[5] and others, that the decussation of the optic tracts in the chiasma is a complete one also in man and the higher animals, this view is demonstrably erroneous in the case of man and the monkey, and also in some other animals, specially the dog and the cat.

Destructive lesion of one optic tract in man[6] causes homonymous hemianopsy of both eyes, by paralysing the corresponding half of both retinæ. Division of the left optic tract, therefore, causes total loss of vision towards the right side.

On two separate occasions, when establishing lesion of the temporal lobe in monkeys, I accidentally severed the optic tract, with the result of causing complete hemianopsy towards the opposite side. In one of these cases[7] the animal lived for eighteen months. The hemianopsy was persistent, and both optic discs exhibited, in course of time, well-marked atrophy in the outer sectors. The opposite optic nerve was only half the sectional area of the other. Though in both cases there

[1] This does not appear to hold in the case of birds, as the owl is pointed to by Michel as having complete decussation, though the fields of vision fall together to a large extent. But I am not aware that anyone has actually experimented on owls in reference to this point, and, even though the complete decussation should be proved in their case, the condition in birds would not invalidate the generalisation as regards mammals. In addition, the recent observations and experiments of Gudden, Munk, and others, referred to in Chap. IX. § 13, render the hypothesis of total decussation, even in pigeons, extremely doubtful. If so, it is much more likely to be erroneous in the case of owls.

[2] *Sitzberich. d. Wien. Acad.*, Bd. xlii. 1860.

[3] *Archiv f. Ophthalmologie*, Bd. xix. 1873.

[4] *Ibid.*

[5] *Von Gräfe u. Sämisch's Handb.* 1874.

[6] Gowers, *Centralblatt f. d. med. Wissensch.* 1878; Nettleship, *Brit. Med. Journ.* 1883, vol. ii. p. 778.

[7] Experiment 25 (figs. 110–116), *Philosoph. Transact.*, Part II., 1884, p. 537.

was also lesion of the corresponding hemisphere, a comparison of similar lesions in other cases showed that the hemianopsy was in relation with the lesion of the optic tract alone. In man and—so far as can be judged—in the monkey the exact half of each retina is paralysed by division of the corresponding optic tract. It is questionable whether the same rule obtains in the case of the cat and dog. The facts rather favour the existence of a relatively larger proportion of cross than direct fibres in these animals. Nicati [1] found that division of the optic chiasma in the middle or sagittal line in cats did not entirely abolish vision in either eye; and Bechterew [2] found that section of the optic tract in dogs caused homonymous hemianopsy in both eyes towards the side opposite the lesion. The partial decussation of the optic tracts is further shown by the secondary degeneration which results from enucleation of the eyeball or division of the optic tract. Baumgarten [3] traced degeneration in both optic tracts in a case of destruction of one eye in man.

The experiments of Gudden,[4] confirmed by those of Ganser,[5] and Monakow,[6] have shown that after enucleation of one eye in cats and dogs partial atrophy occurs in both optic tracts, but to a much greater extent in the tract of the opposite side. The position of the cross and direct fibres in the chiasma and optic nerves is the subject of some differences of opinion, but the view originally propounded by Hannover, that the direct fibres lie on the corresponding side (fasciculus lateralis) of the chiasma and optic nerve, is supported by the results of the experiments above mentioned.

The secondary atrophy of the optic tracts which ensues on enucleation of the eyeball involves the corpus geniculatum externum, the pulvinar of the optic thalamus, and the superficial grey layer and superficial medullary fibres of the anterior tubercles of the corpora quadrigemina (see fig. 49, left side).

In those animals, such as the rabbit, in which the cross

[1] *Centralblatt f. d. med Wissensch.*, 1878.
[2] *Neurologisches Centralblatt*, 1883.
[3] *Centralblatt f. d. med. Wissensch.*, 1878.
[4] *Archiv f. Psychiatrie*, 1870; *Archiv f. Ophthalmologie*, 1874 *et seq.*
[5] *Archiv f. Psychiatrie*, 1882. [6] *Ibid.* 1883.

fibres alone exist (Mandelstamm) or greatly predominate (Gudden) there is marked diminution in these structures on the opposite side as compared with the other. But where, as in the cat and dog, the direct fibres are in larger proportion they are reduced on both sides as compared with those of a normal brain.

Conversely, when the anterior tubercle, pulvinar, and corpus geniculatum externum are destroyed on the one side, atrophy ensues largely in the opposite optic nerve, and partially in the optic nerve of the same side.

The atrophy of the optic tract, which results from extirpation of the eyeball, is exclusively confined to those fibres which are connected with the external geniculate body and anterior brachium of the quadrigeminal tubercles. Those which join the internal geniculate body and posterior brachium remain unaffected, and constitute with those of the other side the inferior commissure (Gudden), which, therefore, though an integral portion of the optic tracts and chiasma, has no direct relation to the optic nerves.

The various facts above mentioned establish, beyond all doubt, the connection between the eyes and the anterior tubercles of the corpora quadrigemina. In a subsequent chapter (Chapter IX.) similar proofs will be given of their relation to the visual centres of the cerebral hemispheres.

§ 4. The differences in respect to the degree of decussation, partial or complete, in different animals will naturally cause differences in the extent of impairment of the field of vision from unilateral lesion of the corpora quadrigemina. In some this lesion will cause total blindness in the opposite eye; while in others there will be homonynous hemianopsy, more or less symmetrical. Presumably also there will be differences as regards the degree of bilateralness of the oculomotor and other reactions excited through each eye. It is universally admitted that section of the optic nerve abolishes the reflex contraction of the pupil to the stimulus of light in that eye. Knoll[1] has shown that in the rabbit, section of the optic tract in any part of its course between the chiasma and the corpora quadrigemina annihilates the reflex contraction

[1] 'Physiologie der Vierhügel,' Eckhard's *Beiträge*, Bd. iv. 1869.

of the pupil in the opposite eye, thereby proving that the centripetal path crosses at the chiasma, and proceeds along the opposite optic tract. Bechterew,[1] however, contends that the centripetal path of reflex pupil constriction is not in the optic tract of the opposite side, but along the wall of the third ventricle of the same side. This opinion he founds on the fact that lesion of the wall of the third ventricle in the dog causes paralytic dilatation of the pupil on the same side, while section of the optic tract at any point posterior to the chiasma does not paralyse the reflex constriction of the pupil in the one eye or the other. But inasmuch as each optic tract is in relation with both eyes, and commissural connections exist between the third nerves and oculo-motor nuclei on each side, it is easy to account for the persistence of irido-motor reaction after such lesions without assuming the existence of any such centripetal reflex path in the wall of the third ventricle. And there is good reason for believing that, in the necessarily coarse operative procedure of establishing lesions in the wall of third ventricle, the centres of irido-motor action defined by the careful and accurate experiments of Hensen and Volckers are directly injured.

We cannot, therefore, place reliance in the experiments or views of Bechterew in opposition to such definite results as those obtained by Knoll. Knoll, however, states—and in this he is confirmed by Bechterew—that destruction of the corpora quadrigemina as such, apart from direct lesion of the optic tract, does not paralyse reflex irido-motor action. He therefore opposes the view maintained by Flourens, Longet, and others that the corpora quadrigemina or optic lobes are the centres of co-ordination between retinal impressions and irido-motor reaction, and ascribes the results obtained by these observers to direct lesion of the optic tracts, or of the oculo-motor nuclei themselves. It is obvious, however, that, though the whole of the optic lobes may not be concerned in reflex irido-motor reaction, there must, in some part of these ganglia, exist paths which connect the optic tracts with the underlying oculo-motor nuclei. Meynert, as above mentioned, looks upon the radial fibres of the corpora quadrigemina as

[1] Pflüger's *Archiv f. d. ges. Physiologie*, Bd. xxxi. 1883.

the probable intracentral connecting links.[1] But, whatever may be their exact position, we are justified in assuming that there are in the region of the corpora quadrigemina fibres of connection between the optic tracts and oculo-motor nuclei, and that the integrity of these connections is a necessary condition of reflex irido-motor and general oculo-motor reaction.

§ 5. But the facts of comparative anatomy would be sufficient to prove that the co-ordination of retinal impressions with oculo-motor reactions is not the only function of the corpora quadrigemina, even if we regard this as an integral portion of their functions.

The corpora quadrigemina or optic lobes stand in no constant relation to the development of the eyes or the oculo-motor apparatus. These ganglia are highly developed in animals in which the eyes and optic tracts are in a very rudimentary condition. Among animals of this kind Longet[2] enumerates various genera of *moles* and *shrews*, in the class mammalia; the *proteus* and *cecilia*, in the class amphibia; and the *Apterichthys cæcus*, and *myxine*, or *hag*, among fishes.

In the mole[3] the optic nerves are excessively small, and the third and fourth nerves are wanting. The optic tracts and chiasma are mainly constituted by Gudden's inferior commissure; yet the corpora quadrigemina are relatively large. The nates, however, though well developed otherwise, exhibit almost total absence of the superficial grey layer and superficial medullary layer—the layers which undergo atrophy when the eyeball of the opposite side is extirpated. These structures

[1] Darkschewitsch (Pflüger's *Archiv f. Physiologie*, Bd. xxxviii. 1886) considers the posterior commissure to be the path of communication between the optic tracts and the oculo-motor nuclei. Section of the posterior commissure in rabbits annihilates the contraction of the pupils normally conditioned by the stimulus of light on the retina. He regards the posterior commissure as consisting of two divisions: a ventral, formed of fibres connecting the optic tract with the opposite upper oculo-motor nucleus and posterior longitudinal bundles through the ganglion habenulæ and its connections; and a dorsal, formed of the decussating fibres of the deep medullary fibres of the anterior tubercles of the corpora quadrigemina in their ascent to the cerebral hemispheres.

[2] *Anat. et Physiol. du Syst. Nerveux*, 1869.

[3] Ganser, 'Vergleichend-anatomische Studien ü. das Gehirn des Maulwurfs, *Morphologisches Jahrbuch*, Bd. vii. 1882.

only appear to be directly related to the optic nerves, and it is these only which are reduced when the eyes are rudimentary. It is evident, therefore, that the corpora quadrigemina have functions, to a large extent at least, independent of the eyes; though it is at the same time clear that these functions are such as are more or less largely influenced by impressions made on the optic nerves. There is an inverse relation between the development of the corpora quadrigemina and cerebral hemispheres; and we might argue *a priori* that the degree of independence of the functional manifestations exhibited by animals after removal of the cerebral hemispheres probably varies with the development of the mesencephalic ganglia, and that these ganglia are therefore an essential part of their central mechanism.

§ 6. Rolando and Serres had observed that lesions of the corpora quadrigemina in various animals gave rise to marked disturbances of equilibrium and irregularity of movement. Cayrade,[1] instituting more careful experiments on the comparative effects of destruction of different parts of the encephalon, found that in frogs, after removal of the optic lobes anterior or posterior to the rudimentary cerebellum, the attitude was no longer normal, as when the hemispheres only were removed. The animals rested on the table with the abdominal surface and inside of the thighs, and when urged to move either merely crawled or, if they jumped, rolled over on their back or side, and with great difficulty righted themselves. When thrown into the water they were able to swim, but without direction and without equilibrium, rolling over and over in the water.

While able to make co-ordinated movements of defence and the like, they had entirely lost the harmony and equilibrium of their movements *d'ensemble*.

Goltz [2] confirmed and amplified the results described by

[1] 'Sur la Localisation des Mouvements Réflexes,' *Journ. de l'Anat. et Physiologie*, 1868.

[2] *Funct. der Nervencentren des Frosches.* Berlin, 1869. Neither Goltz's nor Cayrade's experiments indicate total loss of equilibration after removal of the optic lobes, and Luchsinger (Pflüger's *Archiv*, Bd. xxxiv. 1884) states that even when all the encephalic centres anterior to the rudimentary cerebellum are removed, attempts are made to regain equilibrium more or less successfully.

Cayrade. Frogs deprived of their cerebral hemispheres, optic thalami, and optic lobes were able to spring when urged, but their movements were 'plump und unbeholfen.' Turned over on their back, they managed with difficulty to recover their normal attitude, but the feet were planted irregularly, and the body was supported more by the abdominal surface than by the limbs. Submitted to the balancing experiment before alluded to (p. 109), they were altogether unable to adapt their movements, and fell like a sack of flour when the basis of support was tilted.[1]

That the phenomena are not due merely to the blindness resulting from destruction of the optic lobes is shown by the fact that a frog deprived of its cerebral hemispheres, and also of its eyes, is still able to maintain its equilibrium as before. If the optic lobes alone are destroyed, exact equilibration is impossible, even though all the other encephalic centres are retained. Goltz's experiments were repeated in his laboratory and fully confirmed by Kohts.[2] Kohts observed the same disorders of equilibrium after lesions or destruction of the optic lobes in frogs. Pigeons exhibited rotation and circus movements, oscillated and staggered, and fell helplessly when thrown into the air. Dogs also reeled and tumbled about, planted their feet in irregular positions, and appeared as if profoundly intoxicated.

McKendrick[3] also has observed disturbances of station

Steiner in a recent work (*Physiologie des Froschhirns*, 1884) states that a frog deprived of all its centres above the medulla oblongata is still able to preserve its normal attitude, and to right itself if turned on its back, as well as to jump and swim, though its swimming is not quite normally co-ordinated. All these actions are rendered impossible when a section is made posterior to the cerebellum. The portion of the medulla ventral to the cerebellum (Stieda's pars commissuralis) he regards as the centre of locomotion. Fano's experiments (*Saggio Sperimentale sul Meccanismo dei Movimenti Volontari nella Testuggine Palustre*, 1884) on the tortoise are of a similar nature, essential importance being attached to the integrity of the anterior portion of the medulla oblongata—a region which would correspond to the pons of higher animals.

[1] Steiner (*Physiologie des Froschhirns*) states that destruction of the optic thalami alone has the same effect. Otherwise the destruction of the optic thalami causes little impairment of the other responsive reactions.

[2] 'Zur Lehre von den Functionen der Corpora Quadrigemina,' Virchow's *Archiv*, Bd. lxvii. 1876.

[3] 'Experiments on the Brain of Pigeons,' *Trans. Roy. Soc.* Edin. 1873.

and locomotion as well as blindness after lesions of the optic lobes in pigeons.

In a series of experiments which I made on various animals I observed similar phenomena. In fishes lesions of the tectum, or roof, of the hollow optic lobes caused disturbances of equilibrium, &c.—the animals being unable to maintain the normal attitude, and swimming on one side or the other, or on their back. Entire removal of the optic lobes rendered station and locomotion impossible. The only movements capable of being carried out under such circumstances were mere reflex flaps of the tail on cutaneous stimulation. The phenomena were the same whether the cerebral hemispheres were previously removed or not.

In rabbits disorganisation of the corpora quadrigemina caused blindness, with dilatation and immobility of the pupils, and marked disturbances of equilibrium and locomotion. While still capable of making co-ordinated movements of all four limbs on reflex stimulation, or when held up by the tail, they could neither stand nor walk, but rolled over from side to side. In one animal, in which the whole brain was removed by a section passing just anterior to the junction of the anterior peduncles of the cerebellum with the testes, co-ordinated reflex action of the limbs could be elicited by reflex stimulation for twenty-four hours after the operation; but all attempts on the part of the animal to raise itself, or move away from the irritation, were ineffectual.

In the case of a monkey I established lesion of the anterior tubercles of the corpora quadrigemina in the following manner. A wire cautery was passed in a horizontal direction through the anterior extremity of the left inferior occipital fissure (fig. 67, o_2) calculated to traverse the nates. The result, as was proved by post-mortem examination fifteen hours afterwards (the animal being killed with chloroform), was that the convexity of the nates was sheared off on both sides, the left somewhat more extensively than the right. The lesion was entirely in the quadrigeminal lamellæ, and did not invade the central grey substance of the aqueduct of Sylvius, or the structures situated vertically to this canal. Slight effusion had occurred, with discoloration of the posterior aspect of

both optic thalami; but the posterior commissure was not destroyed, and the corpora geniculata, testes, superior cerebellar peduncles, crura cerebri, and optic tracts were absolutely free from all discoverable lesion.[1] The posterior lobe of the left hemisphere exhibited a blackened horizontal sinus, corresponding to the diameter of the cautery, extending from the point already mentioned on the convex aspect of the lobe across to the anterior extremity of the calcarine fissure. Emerging here it had sheared the nates as above indicated, and the point sank for a line or two into the internal aspect of the opposite hemisphere.

The result of this lesion was that the animal was rendered completely blind. Various tests rendered this clear, among others the fact that twelve hours after the operation it could not discern the position of a dish of milk, placed immediately before its eyes, which it was allowed first to taste, but which it drank with avidity when the dish was held up to its lips. The pupils were dilated and almost, if not entirely, inactive, the left somewhat larger than the right. For some hours the animal kept its eyes closed, except when roused, when it would open the eyes partially as if roused from sleep. There was no ptosis, or distortion of the optic axes, and the eyes were freely opened as the animal recovered. With the exception of sight, all the other senses, general and special, were retained. The animal evidently felt distinctly, and put its hand to any part of the body which was touched or irritated. The power of the limbs was retained, and the animal could grip firmly with both hands and feet. But it was utterly unable to maintain a normal attitude or move steadily. Left to itself it sat in a crouching position with its head bent, and supporting itself by its hands and feet, which were planted in strange and unnatural positions. In this way it sat very unsteadily, swaying backwards and forwards, and especially so when it tried to scratch any part of its body. When it attempted to move it would turn round, generally from left to right, and frequently tended to fall backward, which it counteracted by sudden jerks forward and forcible slaps on the floor with its

[1] These facts, stated in the previous edition, I have again carefully verified by minute examination of the preserved specimen.

tail. The symptoms continued practically unchanged for fifteen hours, after which the animal was killed with chloroform.

Though the blindness observed might be due in part to the lesion of the posterior lobe necessarily caused by the operative procedure in reaching the corpora quadrigemina, yet as similar lesions or even entire extirpation of the occipital lobe on one or both sides may be made without the slightest disturbance of equilibration, we are justified in attributing the disorders of station and locomotion, which were so marked, to the lesion of the corpora quadrigemina as such. Though some authors (Longet,[1] Bechterew,[2] Steiner,[3] &c.) ascribe the disorders of equilibrium observed by so many physiologists to lesion of the subjacent cerebellar or tegmental peduncles and tracts, I do not think that this accords with the facts of experiment, so far as *direct* injury to these tracts is concerned. In fishes the mere breaking up of the walls of the tectum, and in the monkey the destruction of the superficial grey and medullary fibres of the anterior tubercles, without any direct implication of the cerebellar or cerebral peduncles, was sufficient to induce symptoms of the most pronounced character. With the exception of vision, the monkey retained sensation unimpaired, showing that the sensory paths to the hemispheres were unbroken; and that the paths of voluntary motor impulse were similarly uninjured was evident from the manner in which the animal used its limbs. Though it is impossible to separate the lamellæ of the corpora quadrigemina from the tegmental tracts with which they are in relation—and I shall make no attempt to define or limit the extent and influence of a destructive lesion established in this region—it is probable that lesions involving the subjacent tracts cause more marked and enduring disturbances of equilibrium; but that lesions not directly involving these tracts are sufficient to induce marked disorders of equilibrium is, I consider, amply demonstrated by the actual facts of experiment.

Though the disturbances are probably only of an indirect

[1] *Op. cit.*

[2] 'Die Function der Vierhügel,' Pflüger's *Archiv f. Physiologie*, Bd. xxxiii. 1884.

[3] *Op. cit.*

character, they are not without significance in relation to the mechanism of equilibration and other responsive reactions.

§ 7. Goltz found that gentle stroking of the back of frogs no longer excited croaking when the optic lobes were destroyed; and he concludes—and in this he is confirmed by Steiner—that these ganglia are the centres of this emotional responsive action. Longet,[1] however, found that in rabbits and dogs, even after complete removal of the corpora quadrigemina—as well as the hemispheres, corpora striata, and optic thalami—when, therefore, only the pons and medulla oblongata remained intact, irritation of sensory nerves induced general agitation and plaintive cries as of pain; phenomena which entirely ceased when the pons was broken up. Vulpian[2] states that he has obtained exactly the same results, but in the experiment he relates—on a young rabbit—the corpora quadrigemina were not destroyed. He however seems to share the opinion of Longet, that it is the pons, rather than the corpora quadrigemina, which is the centre of these emotional manifestations.

I have found in rabbits that extensive lesions may be made in the corpora quadrigemina without causing cessation of the characteristic cries and other forms of response to general and special sensory stimulation; and Bechterew[3] states that it is only when the optic thalami are destroyed, or sections made posterior to these ganglia, that emotional responsive manifestations cease. This, however, is contradicted by the experiments of Longet and Vulpian, and also by experiments of my own, in which all the centres anterior to the corpora quadrigemina were removed without annihilating emotional response. And I have found in the rabbit that breaking up the optic thalami on both sides did not interfere with the utterance of plaintive and continued cries in response to pinching of the legs or tail, or starting to sounds made in its proximity. In one experiment I removed the whole of the encephalic centres by a transverse section through the posterior margin of the testes. At first on cutaneous stimulation only general reflex movements were induced, without the usual

[1] Quoted by Vulpian, *Physiologie du Système Nerveux*, 1866, p. 541.

[2] *Idem.*

[3] 'Die Function der Vierhügel,' *Neurolog. Centralblatt*, 1883, No. 4.

plaintive cries; but after a few hours cries also were excited. I was unable to perceive any clear difference between the cries in this case and those uttered by an animal in which the corpora quadrigemina were uninjured, though perhaps they were not so long continued or repeated. But this might be explained merely by the greater amount of shock from the severity of the operation.

Probably Bechterew mistakes the effect of shock for the direct results of his operations on the optic thalami. In any case, it is certain that the existence of the optic thalami is not indispensable for the manifestation of such emotional responses as we are considering.

§ 8. The excitability and effects of irritation of the corpora quadrigemina or optic lobes by various stimuli have been differently stated by different observers. Flourens considered that superficially they were not susceptible to mechanical irritation, but that puncture of the deeper layers gave rise to convulsive movements and also contraction of the pupils. My own observations, however, as well as the results obtained by Bechterew, lead me to believe that pure mechanical irritation of the surface of the corpora quadrigemina is capable of inducing distinct indications of excitability. Merely touching these ganglia with a sponge is sufficient to cause general and more or less indefinite movements of the trunk and limbs. The slightest superficial puncture of the corpora quadrigemina in rabbits causes the animals to start suddenly and bound away as if in great agitation and alarm. These symptoms speedily subside, and it is almost impossible to discover any signs of anatomical lesion from the slight puncture which is sufficient to give rise to the manifestations. Much, however, depends on the vital conditions of these ganglia at the time of the experiment. When they are exhausted by shock or hæmorrhage, or paralysed by narcotics, excitation may have little or no perceptible effect. It is doubtless owing to variations of this nature that different observers have arrived at different results. I have made many experiments on the corpora quadrigemina and optic lobes, and have found them extremely sensitive to electrical stimulation with weak induced currents.

On irritation of the nates or anterior tubercles in monkeys I have observed the following results:—Irritation of the one side causes the opposite pupil to become widely dilated, followed almost immediately or accompanied by dilatation of the pupil on the same side. The eyes are widely opened and the eyebrows elevated. The eyeballs are directed upwards and to the opposite side. The head is moved in the same direction as the eyes. The ears are strongly retracted. If the irritation is kept up the tail is elevated, the legs extended, the arms approximated to the sides, drawn back and flexed at the elbows, the jaws clenched, and the angles of the mouth retracted, until a general opisthotonus ensues. The motor effects are shown first on the opposite side of the body, but ultimately both sides become affected by the unilateral irritation.

Irritation of the testes or posterior tubercles causes the same dilatation of the pupils and general motor symptoms, but with these, and as the first effect, the utterance of a short bark or cry on the slightest contact of the electrodes, and every variety of vocalisation when the stimulation is continued

In dogs, jackals, cats, and rabbits the effects are the same, irritation of the nates on one side causing dilatation of the pupils, direction of the eyeballs and head to the opposite side and upwards, trismus, retraction of the angles of the mouth and of the ears, and ultimately opisthotonus.

Irritation of the testes invariably elicited barking or cries of various kinds, in addition to the other phenomena mentioned. Bechterew states that vocalisation in connection with excitation of the testes is not constant, but I have seen no exception to the rule unless when the excitability of the corpora quadrigemina was so reduced by shock, hæmorrhage, or the like that irritation failed also to produce the other characteristic results. So constant is the excitation of cries when the testes are normally responsive, that the utterance of a bark or cry may be regarded as a sign of irritation of these structures when electrical exploration is being made in their neighbourhood.

In pigeons irritation of the one optic lobe causes the opposite pupil to become widely dilated, the head to be moved

to the opposite side and back, the opposite wing to be raised and spread out or flapped, and the feet, especially the opposite one, to be drawn up to the abdomen or occasionally extended.

In frogs irritation of the one lobe causes the head to be thrown back, and to the opposite side, and the legs, especially the opposite one, to be suddenly extended. When the electrodes are placed on both optic lobes at the same time the head is thrown back, the legs extended, and the arms approximated to the sides and rigidly clasped. The pupils do not seem perceptibly affected by slight stimulation, but become widely dilated in the opisthotonic condition. Frequently croaking sounds are likewise elicited.

In fishes (carp) I found that irritation of one optic lobe caused the tail to be struck forcibly and bent to the same side, the dorsal and anal fins being spread out, and pointing in the same direction as the tail, while the pectoral fins were spread out horizontally. I observed no action on the pupils, but usually on irritation the eye of the same side was jerked forwards.

Knoll[1] also has described dilatation of the pupils in connection with irritation of the nates, but, though dilatation of both pupils occurs from unilateral irritation, he is of opinion that the dilatation is greater on the same side. This I have not found to be the case.

§ 9. The explanation of the effects of irritation of the corpora quadrigemina, and of the relation between these and the effects of destructive lesions, is a matter only of speculation. A very commonly followed method of disposing of the results is to attribute them to irritation or lesion of underlying tracts, but those who satisfy themselves with this hypothesis have nothing to say respecting the corpora quadrigemina as such. It is obvious that the corpora quadrigemina are terminal ganglia of very great importance, more particularly in the encephalic system of the lower vertebrates; and it is absurd to suppose that all the manifold results of irritation and lesion of these structures stand in no direct relation to the ganglia themselves, but are only indirect consequences of implication of some indeterminate subjacent or neighbouring centres or tracts.

[1] Physiologie der Vierhügel,' Eckhard's *Beiträge*, Bd. iv. 1869.

Though electrical stimulation is not strictly localisable, and there is always a risk of diffusion, it has been shown that mere mechanical irritation of the surface of the corpora quadrigemina is sufficient to produce motor manifestations, in which case obviously conduction to subjacent or neighbouring tracts can play no part. And in one experiment on a rabbit I observed effects similar to those of electrical stimulation, resulting from inflammatory action. I had endeavoured to injure the corpora quadrigemina through the posterior lobes of the hemispheres, but no immediate results ensued from the operation. After twenty-four hours, however, the animal began to have attacks of trismus and opisthotonus, and all the other symptoms induced by electrical irritation of the corpora quadrigemina. It was found after death that the cautery, with which the lesion was established, had not actually touched the corpora quadrigemina, but had excited inflammatory adhesion of the posterior extremity of the hemispheres to the surface of the nates, which were in an active state of congestion, though not otherwise injured. In this case vital irritation had produced the same effects as the application of the electrical stimulus. The strength of current sufficient to produce active manifestations, when applied to the surface of the corpora quadrigemina, is very weak, and barely perceptible when applied to the tip of the tongue, so that the risk of diffusion is very slight; and it is a fact, which cannot be explained away by mere diffusion to subjacent structures, that irritation of the testes differs from that of the nates in at least one important particular, viz. the excitation of cries of various kinds. These I have never observed on irritation of the nates. If it were merely a matter of diffusion to subjacent tracts the same results should occur in both cases. But there is an anatomical difference between the nates and testes which supports the view that the phenomena are due to the direct excitation of these ganglia as such. The surface of the nates is composed of zonal fibres, superficial grey matter, and medullary fibres, which are directly related to the optic tracts, structures which are not found in the testes. It is these layers only which vary with the development of the optic tracts, and not the corpora quadrigemina as a whole, which,

as we have seen, may attain a high development in animals whose eyes are of quite a rudimentary character. The corpora quadrigemina, as Serres has shown, vary directly with the development of the spinal cord, and inversely with the development of the cerebral hemispheres. They may be regarded as the ganglia of the fundamental spinal system, with which, through the fillet and reticular formation, they are in more or less direct continuity.

Through them the eyes are brought in relation with the fundamental sensory and motor tracts and centres of the spinal cord—a relation which varies with the development of the eyes—and thus is furnished an anatomical basis for the highly complex and diversified responsive reactions conditioned by impressions on the organs of vision. The phenomena which result from irritation, mechanical, chemical, or electrical, of the lamellæ of the corpora quadrigemina or optic lobes appear to be mainly, if not exclusively, of a reflex character, and are such as may result from irritation of sensory centres or tracts. If we assume that in the corpora quadrigemina sensory impressions, retinal and others, are co-ordinated with adaptive motor reactions, such as are involved in equilibration and locomotion, we should scarcely expect to excite these otherwise than in a tumultuous and ungraduated manner by irritation applied to the centres themselves. Though the medulla oblongata is the co-ordinating centre of the respiratory movements, irritation of the centre itself excites only convulsive and irregular action of the respiratory muscles, instead of the rhythmic alternation characteristic of the normal activity of the centre. In the movements of the head, trunk, and limbs, excited by stimulation of the optic lobes of all animals, it is not impossible to trace adaptations in response to retinal impressions; but the convulsions, and the trismus with tetanic retraction of the angles of the mouth, are all phenomena of the same character as may be induced by irradiation of sensory irritation throughout the spinal centres, such as occurs in traumatic or idiopathic tetanus.

§ 10. So also the dilatation of the pupils, which is so readily induced by irritation of the corpora quadrigemina, may be regarded as a sign of irritation of sensory structures. The

same phenomenon occurs on irritation of the posterior columns of the spinal cord and on stimulation of sensory nerves in general. This is a reflex act effected through the medium of the anterior roots of the second dorsal nerves which ascend in the cervical sympathetics. Section of the cervical sympathetics, as has been shown by Knoll, causes cessation of the dilatation of the pupils normally occurring on irritation of the corpora quadrigemina. No direct relation has been satisfactorily established[1] between irritation of the nates and the constringent action of the irido-motor nucleus of the third nerve. This is a fact which favours the views of those who hold that the corpora quadrigemina as such are not the medium of the irido-constrictive reaction induced by stimulation of the retina.

Of a similar nature, i.e. as an expression of sensory irritation, seem to be the cries and various forms of vocalisation elicited by stimulation of the testes. I have observed also cries on stimulation of other sensory tracts, particularly the restiform bodies, but I have never found cries so readily induced as by irritation of the testes. The slightest contact of the electrodes, when the testes are in full activity and unexhausted, is responded to invariably by a sudden bark or cry. It might be suggested not unreasonably that the cries are due to irritation of the quadrigeminal roots of the fifth nerve, which spring from an arch of vesicular cells surrounding the central grey substance of the aqueduct of Sylvius.

These roots have been described by Meynert as belonging to the sensory division of the fifth nerve, and this being admitted, the suggested explanation is apparently not without foundation. But the sensory character of this root has been altogether denied by Henle and Forel, who regard it as belonging to the portio minor or motor division of the fifth. Under these circumstances we cannot say, with any assurance, that the cries elicited by irritation of the testes are merely the result of irritation of the sensory roots of the fifth nerve. Nor would this mode of explanation account for the difference

[1] Bechterew speaks of constriction of the pupils in connection with electrical irritation of the corpora quadrigemina (*op. cit.*) This is obviously an error. All other experimenters have specially noted dilatation.

between irritation of the nates and testes respectively. I have never observed cries on irritation of the nates, and yet diffusion to supposed sensory tracts or roots is equally possible in both cases. Some other mode of explanation of the characteristic differences is therefore obviously needed.

The phenomena occurring on irritation of the nates and testes respectively appear to me to be the result of irritation of these ganglia as such, and not of subjacent tracts, and to depend on the structural differences between the anterior and posterior pairs of tubercles. The nates have, in addition to the structures which form the arch of the testes, layers of white and grey matter, which give origin to and vary with the size of the optic nerves. If we suppose, as appears to me to be the case, that the tracts of common sensation are superficial in the testes, and those of retinal impressions superficial in the nates, it is possible to explain the cries in the former case and their absence in the latter. The cries would be the mere reflex expression of irritation of common sensory structures, irritation of which alone, in contradistinction to those of special sense, gives rise to pain, or its physical expression in the form of screams or cries. Whether, however, there is a special relation between irritation of the testes and the utterance of emotional cries, the hypothesis which I was at first inclined to adopt from the results of the experiments of Goltz, Vulpian, &c. is, I now think, more open to doubt, but not unworthy of consideration. For, though cries may be elicited even when the corpora quadrigemina, as well as higher lying centres, are destroyed, it would not follow that the testes are entirely without influence in this relation.

§ 11. That the phenomena of irritation of the corpora quadrigemina are expressions of sensory stimulation is further supported by the influence which irritation of these ganglia exerts on the circulation and respiration, modifications of which are, as is well known, usual concomitants of states of feeling. Danilewsky,[1] anticipating some of the results of a series of experiments on this subject by Dr. Lauder Brunton and myself, found that electrical irritation of the deeper layers of the corpora quadrigemina caused a great rise in the blood

[1] Pflüger's *Archiv*, vol. xi. 1875.

pressure, with slowing of the heart and amplification of the pulse-waves. With these modifications of the circulation we observed also very marked modifications of the respiratory rhythm; irritation causing a deep inspiration followed by prolonged and powerful expiratory efforts.

Similar modifications of the respiratory rhythm have also been described by Newell Martin[1] in frogs as the result of the application of salt to the cut surface of the optic lobes. Christiani[2] also has described convulsive inspiratory and expiratory movements as resulting from electrical irritation of the walls of the third ventricle immediately anterior to the nates, and of the testes and nates respectively:—expiratory action, according to him, being specially caused by irritation of the nates. These are obviously phases of the same phenomena obtained by Brunton and myself. He applies the term 'centres' to these effective points; a use of the word 'centre' for which there is no justification. The respiratory centres are in the medulla oblongata, and these alone are indispensable for the normal rhythmical alternation of the respiratory movements. The modifications of the respiratory rhythm from irritation of the corpora quadrigemina differ in no respect from the similar effects produced by various degrees of stimulation of peripheral sensory nerves, and are to be regarded merely as reflex manifestations of irritation of sensory regions or tracts. Of a similar nature also we should regard the contractions of the stomach, intestines, and bladder, said by Valentin and Budge to result from irritation of the corpora quadrigemina. It has been shown by Mosso and Pellacani[3]

[1] 'Respiration of the Frog,' *Journal of Physiology*, vol. i. Nos. 2 and 3. In the second of these papers Martin says I erroneously attribute to Danilewsky the discovery of these respiratory modifications from irritation of the corpora quadrigemina. The error is on the part of Martin, not on mine. I distinctly indicated that the point of agreement between Danilewsky's and our results was the effect on the heart and circulation. The modifications of the respiratory rhythm were stated in a separate sentence, and, if perhaps not so clearly expressed as they might be, were founded on our own experiments and graphic tracings, which, however, we did not think it necessary to reproduce, the question being one of very subordinate importance (see *Functions of the Brain*, 1st edition, p. 83).

[2] 'Physiologie d. Kaninchenhirnes,' *Berl. Acad. d. Wissensch.*, Feb. 17, 1881.

[3] 'Sur les Fonctions de la Vessie,' *Archives Ital. de Biologie*, tome i. 1882.

that contractions of the bladder result from irritation of any sensory nerve, and also under all conditions of the organism which raise the blood-pressure and excite the respiratory centres. Under such circumstances contractions of the bladder and the organic viscera, in connection with irritation of the corpora quadrigemina, would be merely concomitants of the other signs of irritation of sensory structures.

From the phenomena occasioned by electrical or other forms of irritation of the corpora quadrigemina or optic lobes it would appear, therefore, that nothing is indicated with any degree of certainty further than the existence of retinal and other sensory tracts or centres, through stimulation of which general motor reactions are capable of being induced. In so far, however, they support the hypothesis, founded on the effects of destructive lesions, that these ganglia form an essential portion of the mechanism of the co-ordination of retinal and general sensory impressions with the mesencephalic motor apparatus concerned in the complex responsive adjustments of equilibration and the other adaptive reactions of which animals are capable after removal of the higher encephalic centres.

CHAPTER VI.

FUNCTIONS OF THE CEREBELLUM.

§ 1. Though there is a more general agreement among experimental physiologists as to the results of lesions of the cerebellum than of any other of the encephalic centres, there seems to be a correspondingly greater difficulty in finding such a definition of the functions of this organ as shall include and satisfactorily explain the immediate symptoms of cerebellar lesion in animals, and the varied, irregular, or latent phenomena of cerebellar atrophy or disease in man. An account of the notions that have been expressed at various times respecting the functions of the cerebellum would form a curious and entertaining chapter, but only those are seriously worthy of consideration here which are based on reliable experimental or clinical methods.[1] These commence with the classical researches of Flourens.[2] Flourens thus describes the results of one of his experiments on pigeons: 'I removed the cerebellum of a pigeon in successive slices. On removal of the superficial layers there appeared only a weakness and want of harmony in its movements. On removal of the middle layers it exhibited general agitation without convulsions. The movements were brusque and irregular, but sight and hearing were unaffected. On further destruction the animal entirely lost the power of leaping, flying, marching, or maintaining the upright position, which had been gradually impaired by the previous injuries. Placed on its back it was unable to rise. But,

[1] On this ground I do not consider it necessary to discuss the most widely known but least well founded of all the hypotheses as to the functions of the cerebellum, viz. that of Gall, which regards this organ as the seat of the sexual instinct.

[2] *Recherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux*, 1st edit. 1824; 2nd edit. 1842.

instead of remaining quiet and still like pigeons deprived of their cerebral hemispheres, it was in a continual state of restlessness and agitation, but its movements were never firm or determinate. It could see a threatened blow, and endeavoured to avoid it, but only made a thousand useless contortions. It made numerous ineffectual efforts to recover its upright position when laid on its back, but became exhausted with its struggles, and remained as it was placed. Sensation, volition, and intelligence were retained, the possibility of making *mouvements d'ensemble* persisted, but the co-ordination of these movements into regular and determinate movements of locomotion was lost' (p. 37).

Numerous similar experiments on pigeons and other birds gave essentially identical results. In all cases lesions of the cerebellum induced disturbances of station and locomotion, varying from the swaying and reeling of slight intoxication to the most profound and indescribable confusion, according to the extent of the injuries inflicted. In no instance did sensation or intelligence appear to be affected; and, in fact, the retention of these faculties kept up and intensified the vain and tumultuous struggles. In mammals also (cats, dogs, moles) Flourens demonstrated the occurrence of similar phenomena. Slight or superficial lesions of the cerebellum caused some disharmony of movement—a disharmony which became more pronounced in proportion to the extent of the lesion—while complete destruction of the cerebellum rendered station and locomotion altogether impossible. He concluded from his facts that there exists in the cerebellum a 'propriété qui consiste à *coordonner* les mouvements *voulus* par certaines parties du système nerveux *excités* par d'autres.'

§ 2. Taking the experimental data alone, apart from Flourens' interpretation of them, we find that they have been thoroughly confirmed by all who have performed similar experiments on birds and mammals; and we may take as an established fact that lesions of the cerebellum in these animals, in the first instance at least, cause disorders of movement resembling those of intoxication in varying degree.

In respect to the lower vertebrates—fishes and frogs—the results of lesions of the cerebellum have been stated somewhat

differently by different observers. Vulpian [1] and Philipeaux did not observe any appreciable disorders in the movements of fishes unless the peduncles of the cerebellum were injured, in which case the phenomena were similar to those observed in birds and mammals. Reñzi,[2] however, found that lesions of greater or less extent, confined to the cerebellum, caused in fishes precisely the same kind of disturbances of equilibrium and locomotion as Flourens described in birds and mammals. Dickinson [3] also, in a series of careful experiments, in which he established lesions in the cerebellum of perch, dace, and goldfish, found that in every instance there were marked disorders of equilibrium. The animals invariably showed loss of lateral balance, oscillated from side to side, or rolled round and round when they swam. In many similar experiments which I made on goldfish, in which I satisfied myself by post-mortem examination that the lesions were accurately confined to the cerebellum, I found that the animals continued able to swim, but never in the normal attitude, but belly upwards, or on one side or the other. Dickinson also found that if only the medulla and spinal cord were left uninjured in fishes the maintenance of the erect posture and locomotion were impossible; but if the cerebellum remained also, they were able to maintain a steady though not always erect posture, and to move along in the water with the aid of the tail and trunk, while the anterior fins remained motionless.

Lesions or removal of the rudimentary cerebellum of frogs and toads appear to cause no very evident disturbances of equilibrium or locomotion. They continue able to preserve their normal attitude and to regain it if they are forcibly turned over. They crawl or leap if stimulated, but they are somewhat unsteady, and do not recover themselves so readily. Tortoises, according to Dickinson, exhibit a loss of activity and a stiltedness of gait after removal of the cerebellum; and snakes show a loss of lateral balance.

[1] *Leçons sur la Physiologie du Système Nerveux*, 1866.

[2] 'Funzioni di Cervelletto dei Pesci,' *Annal. Univ. di Medicina*, vol. clxxxv. 1863, p. 486.

[3] 'Functions of the Cerebellum,' *Brit. and Foreign Med.-Chir. Review*, Oct. 1865.

§ 3. It is shown by the foregoing experiments with a remarkable degree of uniformity in all classes of animals that mechanical lesions of the cerebellum induce, in the first instance at least, such disorders of equilibrium that station or locomotion becomes difficult and sometimes altogether impossible. It is not that the muscles are paralysed, or that the co-ordinated movements of the limbs cannot be made—for these may be willed or excited as before—but they are no longer co-ordinated with those necessary to the normal position of the body in space, and hence the animal, in its attempts at locomotion, reels, staggers, or flounders about in the most helpless manner. As to the intensity and duration of these disorders, however, much depends on the extent and suddenness of the lesions. Flourens found that superficial lesions, or even deep incisions into the substance of the cerebellum, might be ultimately recovered from, the animals regaining complete stability and steadiness in their movements. After complete removal of the cerebellum, however, birds never entirely recovered, but manifested the characteristic symptoms of cerebellar lesion during the several months of their survival. Dalton [1] observed in a pigeon, in which he had destroyed about two-thirds of the cerebellum, at the end of sixteen days only a general debility and slight difficulty in recovering itself when it alighted from flight. Immediately after the operation the characteristic titubation was, however, as usual, well-marked. In two others, in which about half the cerebellum only was destroyed, no symptoms were clearly evident after a similar period of survival. Wagner [2] also saw complete recovery in a pigeon which survived twelve weeks after extirpation of more than a half of the cerebellum. But in those in which the lesions extended into the corpora dentata complete recovery did not occur. There was a tendency to over-action of the extensors, torsion of the head and neck, and general muscular tremors, especially intensified by disturbance of any kind. Weir Mitchell [3] could only detect a general

[1] *Amer. Journ. of the Med. Sciences*, Jan. 1861.

[2] 'Rech. sur les Fonctions du Cerveau.' Trans. in *Journ. de la Physiologie*, 1861.

[3] *Amer. Journ. of the Med. Sciences*, April 1869.

feebleness and incapacity for prolonged exertion in a pigeon which survived for several months after destruction of the greater portion of its cerebellum.

As a rule, mammals do not long survive extensive mutilation or destruction of the cerebellum. But recently Luciani [1] has obtained remarkable results in this respect. One bitch lived for eight months after nearly complete extirpation of the cerebellum. At first there were signs of inflammatory complications, indicated by contractures and spasms; but after six weeks these subsided, and the animal, otherwise well, exhibited till death the characteristic unsteadiness and titubation of 'cerebellar ataxy.' Notwithstanding the anomalies in locomotion, the animal when thrown into the water was able to swim, with well co-ordinated movements of the limbs, and head erect like a normal dog. She was, however, unable to land when she had reached the side. The animal was in full possession of all its senses, expressed its emotions in a perfectly natural manner, and, what is of interest in reference to the phrenological hypothesis, manifested 'heat' at the usual autumnal period, though coitus could not be effected owing to the motor instability. In the later months of life the animal suffered from purulent otitis, catarrhal conjunctivitis, affections of the joints, and general malnutrition, of which she died.

In a second still more remarkable case—also a bitch—the cerebellum was removed in two operations eleven months apart, and between these two operations the sigmoid gyri of both hemispheres were likewise destroyed. The animal, having manifested 'heat' and been impregnated four months after complete extirpation of the cerebellum, was allowed to survive until she had whelped, nearly a year after. Parturition was quite normal, and the maternal instincts were exhibited in all their natural intensity and solicitude. The animal was in excellent health and

[1] 'Linee generali della Fisiologia del Cervelletto, Prima Memoria.' Firenze, 1884. Also an oral communication to the Italian Phreniatric Society, September 1883, translated by Workman in the *Alienist and Neurologist* for July 1885. This memoir contains facts of a later date than those recorded in Luciani's 'Prima Memoria.'

nutrition—unlike the first—and had increased in weight. She was killed by chloroform, and the brain examined by a committee to whom she was entrusted. Only a small fragment of the right lobe of the cerebellum existed, and the sigmoid gyri had been destroyed in both hemispheres.

In this animal there were few, if any, signs of inflammatory complications, and no metastatic abscesses. But, unlike the first, which was able to stand and walk, though unsteadily, this animal was never able to stand erect or to walk, and could only move from place to place by butting forward and proceeding by the force of her falls. The head also was subject to continual oscillations when she tried to mouth anything. Though unable to stand up or to walk, she was able to swim, with however some tendency to inclination to one side. Except for the disorders of station and locomotion the animal exhibited no other anomaly.

These two experiments prove satisfactorily that destruction of the cerebellum in the lower mammals is followed by long-continued if not permanent disorders of equilibrium. But the records of cerebellar disease in man are of a most conflicting character in respect to this question, and it is far from easy to harmonise them with each other or with the established facts of experimental physiology.

§ 4. The most characteristic symptom of cerebellar disease in man, apart from indirect complications, is an uncertain or reeling gait, like that of alcoholic intoxication. But this symptom, though general and pathognomonic, has not always been obvious, though, as has been proved by post-mortem examination, disease of considerable extent has existed in the cerebellum during life. Unless the disease has been of a sudden character none of the violent and tumultuous disorders which characterise the abrupt lesions of physiological experiment have been met with, and this is a fact which the gradual subsidence of the symptoms in the lower animals would lead us to expect. And we should also be prepared to find that limited lesions might run their course without manifest symptoms, inasmuch as experiments on the lower animals show that under such conditions there may be no appreciable disturbances of equilibrium after a time. And,

as a matter of fact, it is only when the disease has been of comparatively limited extent, or confined to one lobe of the cerebellum, that there has been an absence of the characteristic symptoms. But when the whole cerebellum has been involved by disease, or has been found greatly or completely atrophied, careful observation has never failed to discover a greater or less degree of awkwardness of movement and instability of equilibrium. Many of the cases of atrophy of the cerebellum on record have been found in imbeciles, but it is clear from other evidence that the imbecility or impaired intelligence is only a symptom of cerebral defect coincident with that which has led to the cerebellar atrophy.

The most remarkable case is that of Alexandrine Labrosse, reported by Combette.[1] This girl lived to the age of eleven years, and it was found after death that the cerebellum was entirely atrophied, its place being occupied by a cyst containing serum. Physically she was well developed for her age, but she was five years of age before she was able to stand; and at the age of seven she was very insecure on her legs, and often fell. Her intelligence was defective and her articulation indistinct, but all her sensory faculties were normal.[2]

[1] *Revue Médicale*, tome ii. 1831.

[2] The brain has been figured by Cruveilhier, Liv. XV., Plate V. An almost equally remarkable brain has been recently submitted to me for examination by Drs. Shuttleworth and Taylor, of the Royal Albert Asylum, Lancaster. It was that of a girl who died of phthisis at the age of fifteen. She was under observation in the asylum from December 1882 to March 1884, but nothing was ascertained respecting her early life. She was somewhat weak in intellect, but not to any great extent, and had the narrow palate of the imbecile. Owing to this her articulation was somewhat indistinct. No deficiency existed as regards her sensory faculties, general or special, and the only peculiarity observable in her motor powers was a general muscular weakness and tremor of the hands when she was using them, but this was attributed to the debility associated with her phthisical condition. But she could walk well and steadily, though she was never known to run.

After death no abnormality could be detected in the cerebrum, which was well developed (the whole brain weighing 42 ozs.), but the cerebellum was of the most diminutive character. The left lobe was a mere papilla, the vermiform process a minute nodule obscurely marked with laminæ; while the right lobe, which constituted the main portion, was only half a square inch in superficial area and only a quarter of an inch in thickness at its base. This Lilliputian lobule had, however, the normal laminated appearance and structure.

The pons was indicated by only a few transverse fibres, which barely con-

§ 5. It is evident from this and similar cases that, though cerebellar disease in man is frequently associated with similar symptoms to those which result from experimental lesions in the lower animals, yet the organ may be almost entirely degenerated without any more obvious symptoms than a greater or less degree of unsteadiness of movement or instability of equilibrium. If the cerebellum were indispensable, according to the doctrines of Flourens, for the co-ordination of movements, it would be impossible to harmonise the actual facts of clinical observation with an hypothesis so formulated. For it should have been impossible for Alexandrine Labrosse to walk at all if the co-ordinated movements of locomotion were dependent on the cerebellum. Nor could Luciani's dogs have been able to swim. If, however, we regard the cerebellum as an organ of equilibration it will be possible to bring all symptoms, acute and chronic, into harmony with this hypothesis.

Owing to the gradual subsidence, and in many cases apparently complete cessation, of the symptoms resulting in the first instance from lesions of the cerebellum, it has been

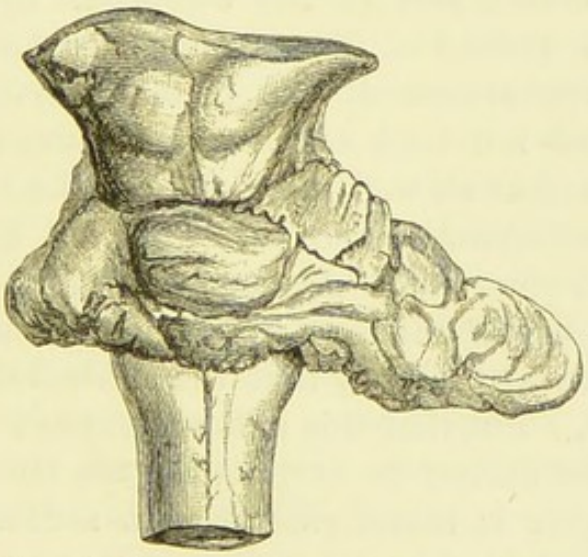


FIG. 51.—Congenital Atrophy of the Cerebellum. Shuttleworth's case. (From a photograph, natural size.)

cealed the pyramidal tracts in their course from the foot of the cerebral peduncles. The corpora quadrigemina had a normal size and appearance. The olivary bodies of the medulla oblongata were only obscurely indicated. With the exception of the cerebellum and its peduncles, which were reduced to insignificant dimensions, the rest of the brain and all the cranial nerves were perfectly normal in appearance.

argued by Brown-Séquard[1] that the phenomena are merely the expression of irritation of nerve centres or structures, and of no more specific relation to the cerebellum as such than, *e.g.*, the convulsions or other nervous symptoms which may be excited by intestinal irritation. It is always a matter of importance to distinguish between the direct and indirect effects of artificial lesions or diseased conditions, and Brown-Séquard truly observes that the frequent neglect of this capital distinction has done much to propagate erroneous notions in cerebral physiology. But that the disturbances arising from lesions of the cerebellum are only due to mechanical or indirect irritation of neighbouring or subjacent tracts or centres, is clearly disproved by the fact that precisely identical results are obtained by methods which cause no mechanical disturbance, such as freezing by ether spray, or destruction of the cortex by the actual or potential cautery.

But though the strictly localised influence of the lesion is maintained by Vulpian and Weir Mitchell, against the vague indeterminate disturbance theory of Brown-Séquard, both these physiologists attribute the phenomena to irritation rather than destruction of the cerebellar tissue; and this mainly on the ground of the gradual subsidence or ultimate complete disappearance of the primary symptoms. This, however, would not be a necessary conclusion, even if the assumption were at all well justified, that the lesions in question were of an irritative nature. But that this is not so is apparent from other considerations. To ascribe the effects of mechanical injury of the cerebellum, such as cutting, tearing, &c. to irritation is to imply that the cerebellum is mechanically excitable. But that this is not the case is clearly shown by the fact that during the very act of such mechanical injury no sign whatever is manifested even in animals which have not been narcotised.

When a nerve, which is mechanically excitable, is cut with a pair of scissors, there is at the moment of section a contraction of the muscles which it supplies. But beyond the momentary contraction there is no further sign of irritation. The subsequent phenomena are those only of paralysis or loss

[1] *Journal de la Physiologie*, tome v. 1862, and elsewhere.

of function. It is only on the setting in of active inflammatory processes, after many hours, that the severed nerve may again become irritated and excite muscular spasms. No such sequence occurs from mechanical injury of the cerebellum. At the moment of infliction there is absolutely no sign whatever, and the greatest violence of the motor disorders is exhibited long before any inflammatory complications can possibly occur, and, if the lesion is established antiseptically, without any inflammatory complication whatever.

Similarly in regard to the influence of the actual cautery. The application of the heated iron at once carbonises the tissues. Neither in the case of the cerebrum nor of the cerebellum is there the slightest sign of irritation, but if the motor centres of the cerebrum have been so treated, there is at once paralysis on the opposite side, and if the cortex of the cerebellum has been destroyed, the characteristic disturbances of equilibrium. If in the one case—and this will be abundantly proved—we have the phenomena of a destructive lesion, we have them as clearly in the other. If there is one method *par excellence* of lowering and temporarily annihilating the function of any living tissue, one would regard freezing as such. And yet Weir Mitchell, who has frozen the cerebellum of pigeons, and observed all the effects described by Flourens in consequence, endeavours to find in the congested state of the vessels, which results from the freezing, a cause of the irritation which he, on other grounds, but unnecessarily and, in my opinion, erroneously, assumes to be at work.

I shall endeavour to show that irritative and destructive lesions are both capable of inducing disturbances of equilibrium, and that the phenomena are quite opposed to each other. Without, however, for the present, attempting to differentiate between irritative and destructive lesions, we may regard it as sufficiently well established that disorders of equilibrium result from cerebellar lesions as such, apart from indirect injury to neighbouring structures.

§ 6. Whether the disturbances of equilibrium vary with the position and extent of the cerebellar lesion is a question of great importance, but one not easy to determine accurately. Owing to the numerous difficulties in experimentation which

have to be encountered, the results are not free from discrepancy. It would seem that when the cerebellum is divided exactly in the median line in an antero-posterior direction, or lesions established as nearly as possible symmetrically on both sides, the disorders of equilibrium are comparatively slight. When the lesions, however, are unsymmetrical or unilateral, the disorders of equilibrium are more manifest, and they vary in character according to the position of the lesion.

It is stated by Flourens and Renzi [1] that lesions of the anterior part of the middle lobe cause a tendency to fall forward, and never backwards; while lesions of the centre and posterior region cause the head to be drawn backwards, and a

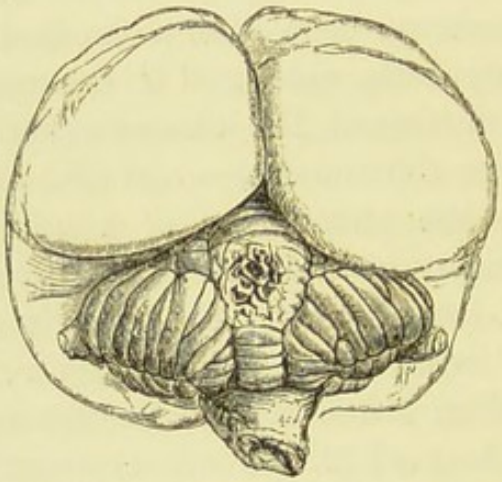


FIG. 52.—Lesion of Posterior part of Median Lobe of Cerebellum of Monkey. (From a photograph, natural size.)

continual tendency to fall supine. This tendency to fall backwards, from lesion of the posterior part of the middle lobe, is well exemplified by the facts of the following experiment on a monkey. The cerebellum was exposed by a trephine opening over the torcular Herophili, and the membranes carefully divided without laceration of the venous sinuses. The posterior part of the median lobe (declive monticuli, fig. 52) was cauterised with a red-hot wire.

Immediately on the operation the animal's head was drawn back in tonic spasm. This lasted only a few seconds, and the animal, on recovering from the narcotic stupor, on attempting to stand, fell supine. It could sit up holding on to some support with its hands, but on letting go tended con-

[1] *Annali Universali di Medicina*, vol. clxxxvii. 1864.

stantly to fall, and frequently did fall on its back. When it tried to run, it always tended to stagger or fall backwards. This tendency to fall backwards lasted during the day of the operation and nearly the whole of the next day, when it was chloroformed to death in order that the exact position and extent of the lesion might be examined. It was found *post mortem* that the lesion was accurately circumscribed to the posterior part of the median lobe, the cortex of which was destroyed over a small circular area (see fig. 52). No other lesion existed in the cerebellum or other part of the brain.

When the lateral lobe of the cerebellum is injured, or the middle peduncle divided, equilibrium is overthrown laterally, and the animal rotates on its longitudinal axis. Some differences of opinion exist as to the direction of the rotation after such injuries, but it was found by Magendie—and his statements have been confirmed by Renzi, Schiff, and many other physiologists—that division of the middle peduncle caused the animal to revolve on its axis with incredible rapidity towards the side of section. Thus if the left peduncle were cut, the animal turned over and over from right to left. Animals so operated on when placed among straw turned so incessantly as to coil themselves up in the straw like bottles packed for transit.

When the rotation is about to occur there is usually observed a very remarkable torsion or spiral twisting of the head and trunk, which seems to carry the animal irresistibly round on its longitudinal axis. Thus on division of the left peduncle the head twists backwards and to the right, the left side of the face looks downwards, the dorsal aspect of the spine tends to the left and downwards, so that the thorax and the fore limbs are directed upwards into the air. The result of this is to cause the animal to roll round from right to left. This rotation is associated with a peculiar deviation of the optic axes. The eye on the side of section looks downwards and inwards, while the eye of the sound side looks upwards and backwards. The upward and backward direction of the right eye coincides with the torsion of the neck backwards and to the right, which with the torsion of the spine above described results in the rotation of the whole body to the left.

This, however, is to be understood of an animal supported on four limbs with the vertebral axis parallel to the ground, as in rabbits. The same animal if pivoted on its hind limbs would then be seen to spin on a vertical axis, and, viewed from the front, would seem to revolve from left to right. We should therefore expect that in man, in whom the body axis is vertical, the same lesion which causes a quadruped to roll round and round towards the left would cause an apparent spinning round from left to right. If the individual were placed on the ground in the position of the quadruped the same impulse which causes the rotation on a vertical axis from left to right would cause the body to roll towards the left side. This apparent difference in cases which are really identical may perhaps serve to account for some of the discrepancies which exist as to the direction in which the equilibrium is overthrown after lesions of the lateral lobe.

We may assume section of the middle peduncle to be equivalent to destruction of the whole of the lateral lobe, and the effects are in reality identical, as has been found by Hitzig. Hitzig found that when the lateral lobe was very extensively injured, the animals rolled over and over to the side of lesion with as great force as in Magendie's experiment on the peduncle itself.

But other experimenters have not always observed rotation towards the side of lesion. Much appears to depend on the extent and situation of the lesion. If the lesion affects the whole of the lobe, the tendency is to roll over towards the affected side, i.e. to revolve on a vertical axis towards the sound side. If the lesion is less extensive, the disturbance of equilibrium may not be so severe as to cause rotation, and the animal may fall towards the opposite side.

Thus I exposed the left lateral lobe of the cerebellum in a monkey, and by means of the actual cautery destroyed the surface of the posterior superior lobule (fig. 53), to the depth of a quarter of an inch, the lesion, as was ascertained by post-mortem examination, being localised exactly in this region. At first the disturbance of equilibrium was very great, the animal tending to fall backwards and to the right; but this movement was sometimes so strong, and combined with spinal

rotation, as to cause the animal to roll over on its left side. On repeated examination for a period of twenty-four hours, I found that the tendency to fall backward and to the right continued whenever the animal attempted to move. This experiment, therefore, shows that a lesion which may cause a tendency to roll towards the same side may in a less degree cause a tendency to fall backwards and to the opposite side.

§ 7. Though the cerebellum, like the cerebral hemispheres, does not respond to mechanical irritation, I found that the application of the induced current to the cortex of the cerebellum in rabbits, after the manner employed in the investi-

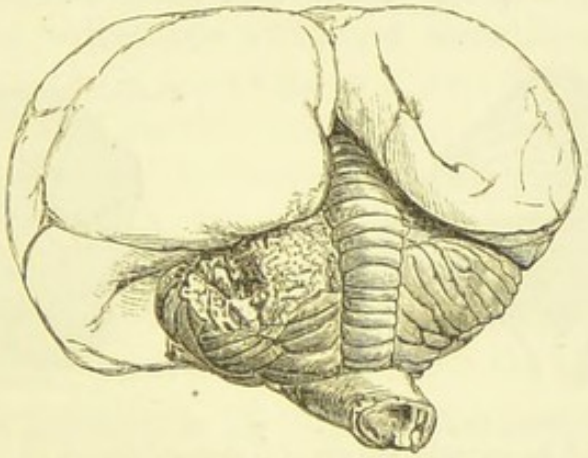


FIG. 53.—Lesion of Left Lateral Lobe of Cerebellum in a Monkey.
(From a photograph, natural size.)

gation of the cerebral hemispheres (see Chapter VII.), caused a remarkable series of ocular combined with other movements, varying according to the point stimulated. Subsequent similar experiments on monkeys and other animals induced similar phenomena; and though many experiments were unsuccessful, owing to the great mortality attending the operations, I succeeded in obtaining a comparative series of observations in a considerable number. The results are such as to bring out the relation of the ocular movements to those necessary for the adjustment of the equilibrium generally.

Electrisation of the Cerebellum of Monkeys.

The cerebellum in the monkey is so overlapped by the cerebral hemispheres that it is impossible to expose it completely in any one case for experimentation. The following

results have been obtained from experiments, more or less successful, on twelve monkeys, though only partial explorations could be made in some of them. The parts most accessible are the vermiform process and the superior and posterior aspect of the lateral lobes, though occasionally other regions were reached, as will be seen from the description.

1. Pyramid of the Median Lobe (Pyramis Vermis) (fig. 54, 1).—*Both eyes turn to the left or right in a horizontal plane*, according as the electrodes are applied to the left or right side of this part throughout its whole extent.

2. Upper Vermiform Process—posterior extremity (Declive Monticuli) (fig. 54, 2).—*Both eyes move straight downwards*,

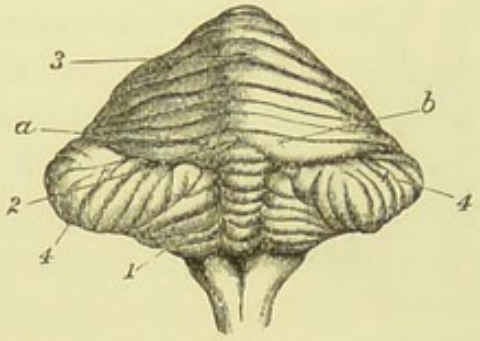


FIG. 54.—Cerebellum of Monkey seen from above and behind. 1, pyramid of the median lobe. 2, declive monticuli or posterior extremity of the superior vermiform process. 3, monticulus cerebelli or anterior extremity of superior vermiform process. 4, postero-superior (semilunar) lobule of the lateral lobe of the cerebellum. (For further significance of numerals see text.)

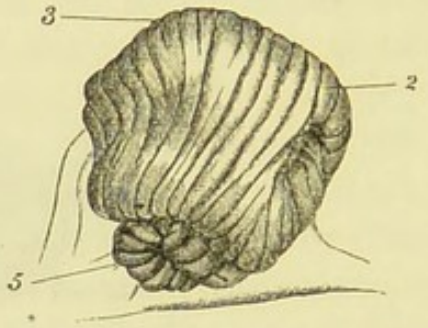


FIG. 55.—Cerebellum of Monkey seen from the left side. 2, the declive monticuli. 3, the monticulus cerebelli. 5, the flocculus.

when the electrodes are applied directly on the middle of this prominence.

a. Declive Monticuli (left side) (fig. 54, *a*).—*Both eyes move downward and to the left.*

b. Declive Monticuli (right side) (fig. 54, *b*).—*Both eyes move downward and to the right.*

3. Upper Vermiform Process—anterior extremity (Monticulus cerebelli) (fig. 54, 3).

a. Middle line.—*Both eyes move directly upwards.*

b. Left side.—*Both eyes move diagonally upwards and to the left (no rotation).*

c. Right side. *Both eyes move diagonally upwards and to the right (no rotation).*

4. Lateral Lobe—Semilunar lobule (fig. 54, 4).

Left side.—*Both eyes move upward and rotate to the left.*

Right side.—*Both eyes move upward and rotate to the right.*

These results were obtained by frequent experiments in this part, and with a remarkable degree of uniformity, there being apparently no further differentiation of special centres in the posterior aspect of the lateral lobe.

Flocculus (fig. 55, 5).

I have only on two occasions been able to place the electrodes successfully, and without complication, on this region. *Both eyes rotate on their antero-posterior axes.*

The vertical meridians remained parallel, the upper extremity moving sometimes with, and sometimes contrary to, the hands of the clock, according as the electrodes were shifted to different parts of the floccular region ; but the exact situation of the electrodes in each case could not be accurately made out.

§ 8. Besides these ocular movements, certain movements of the head and limbs were likewise produced.

In some of my experiments, in which the head was maintained in a fixed position, so that the eyes might be watched conveniently—a method which I had adopted in my experiments on rabbits—only movements of the eyes and limbs, if any, could be noted ; but when the head was allowed free play I found that the movements of the eyes coincided with movements of the head.

Thus, on irritation of the anterior part of the middle lobe (monticulus), when the eyes moved upward the head was thrown back. Occasionally a tendency to extension of the legs was observed, and some spasmodic movements of the arms, the extent and character of which could not be satisfactorily defined.

It may be said that the backward extension of the head and limbs was in reality due to conduction of the current to the corpora quadrigemina, irritation of which causes this effect in a very marked manner ; but that this is not so is proved by the fact that irritation, conducted or directly applied to the testes, invariably excites a sudden bark or howl. This I have occasionally observed when, on irritating the anterior

part of the cerebellum, I had accidentally approached too near the testes. This sudden outcry is a good test of the localisation or not of the irritation on the cerebellum itself. Hence, in the absence of such manifestation, it is to be concluded that the throwing back the head, and the upward movement of the eyeballs, is the distinct result of irritation of the anterior part of the middle lobe of the cerebellum itself, apart from conduction.

The downward movement of the eyes, which results from irritation of the posterior part, or declivity, of the upper vermiform process, is associated with a forward or downward movement of the head. The upward and outward (to the left or right) movement of the eyes resulting from irritation of the posterior-superior lobes is accompanied with a backward and upward movement of the head, to the right or left, according as the right or left side of the cerebellum is stimulated.

With these movements of the head and eyes there are generally associated some movements of the limbs on the same side of the body, *e.g.* on the left side when the left half of the cerebellum is irritated; but their exact character or extent it is extremely difficult to define, owing to their sudden and spasmodic character.

Along with these effects the pupils were observed to become contracted on irritating the cerebellum. The contraction of the pupil is specially marked on the eye of the same side, and I have observed the pupil, on the side corresponding to the half of the cerebellum exposed, remain contracted after the irritation by the electric current had been suspended for some time.

I have never observed any vomiting or sign of excitement of the generative organs in any of the animals experimented on, though I have specially directed my attention to these points.

It is also to be noted, in reference to electrical irritation of the cerebellum, that occasionally stimulation is absolutely without effect at first, and that after the lapse of some time the phenomena follow with great precision. I have not been able to satisfy myself, with respect to these variations, as to whether they depend on degrees of anæsthesia, or state of shock or not. From whatever cause, the excitability of the cerebellum is subject to variations which render the investi-

gation troublesome, and, unless sufficient care is taken, may easily lead to apparently contradictory results. Frequently after the application of the electrodes, a condition of nystagmus comes on and lasts for some time, so that unless due time is allowed for the subsidence of this irritation the results of applying the electrodes to another part become so confused with the effects of the preceding that analysis is impossible. The results above described are those which I have obtained after careful repetition on different animals, and with due regard to those precautions which I have indicated as being necessary.

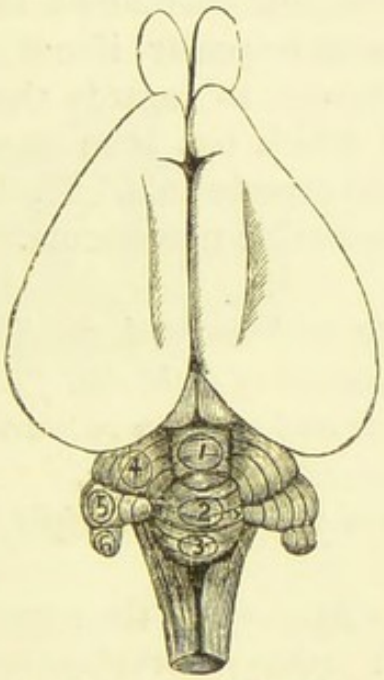


FIG. 56.—Upper Surface of Cerebrum and Cerebellum of Rabbit. The signification of the numerals is given in the text.



FIG. 57.—Anterior aspect of Cerebellum of Rabbit. E is on the cut surface of the pons Varolii. The signification of the numerals is given in the text.

§ 9. *Electrisation of the Cerebellum of Rabbits.*

The following results were detailed in the 'West Riding Asylum Reports,' vol. iii. 1873.

The cerebellum of the rabbit is divided into a number of lobules, more distinctly differentiated from each other than in the case of the monkey and other higher animals. I do not attempt a homological nomenclature, but simply describe the results in reference to the position of the electrodes, as indicated in the accompanying figures (figs. 56 and 57).

Median Lobe.

Upper part (1).—*Both eyes move to the right in a horizontal plane.*

Middle part (2).—} *Both eyes move to the left in a horizontal*
Lower part (3).—} *plane.*

From these results it would appear that the various divisions of the middle lobe differ in action as regards the lateral movements of the eyes. There is, however, no differentiation in the corresponding part of the brain of the monkey, the movement to the right or left depending on whether the electrodes were applied to the right or left side. I have not again verified these results on the rabbit, and therefore it is not improbable that these differences may be partly, if not entirely, due to the position of the electrodes as regards the middle line, a point the importance of which has been more particularly brought out in subsequent experiments. The essential fact, however, is the plane of the ocular movements.

Lateral Lobe.—Left side.

Upper Lobule (4).—*Upwards with inward rotation of left eye; downwards with outward rotation of right eye.*

Middle Lobule (5).—*Upwards and rotation outwards of left eye; downwards and rotation inwards of right eye.*

Lower Lobule (6).—*Both eyes rotate to the right on their antero-posterior axes.*

Anterior Lower Lobule (7).—Apparently the reverse rotation to that described under (6). (One observation only.)

(8).—Anterior part of the Cerebellum. (Position not exactly defined.) (One observation only.) *Both eyes moved upwards*, and then oscillated upwards and downwards.

Besides these ocular movements, protrusion of the eyeballs and increased convexity of the cornea were noted, and also some dilatation of the nostrils.

Another recent experiment, without attempt at definite localisation, confirmed the fact of ocular movements, and also showed that movements of the limbs occurred on the same side as irritation. Twitching of the ears was also observed to occur during stimulation.

The general fact of movements of the eyes, limbs, nostrils, and ears was also noted in some experiments on the cere-

bellum of rats. Localisation experiments were not, however, carried out on these animals.

I have also instituted experiments on the cerebellum of the cat and dog; several unsuccessfully, but in a few with a considerable degree of success as regards the extent of exploration and definiteness of the results.

§ 10. *Electrisation of the Cerebellum of Dogs.*

Median Lobe.

1. Pyramid (fig. 58, 1).

a. Left side.—*Both eyes move to the left.*

b. Right side.—*Both eyes move to the right.*



FIG. 58.—Cerebellum of the Dog, seen from behind and above. 1, pyramid of the middle lobe. 2, posterior extremity or declive of the superior vermiform process. 3, monticulus. 4, postero-superior lobule of the lateral lobe of the cerebellum.

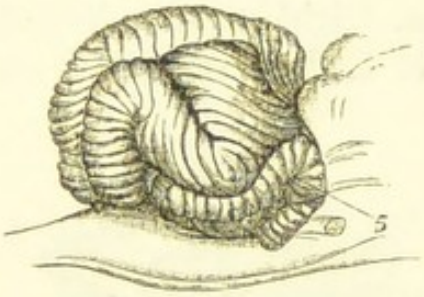


FIG. 59.—Right side of Cerebellum of Dog. 5, the flocculus.

Upper Vermiform Process.

2. Posterior Extremity (declive) (fig. 58, 2).

a. Middle.—*Both eyes move downwards.*

b. Left side.—*Both eyes move downwards and to the left.*

c. Right side.—*Both eyes move downwards and to the right.*

3. *Lateral Lobe.*

4. Postero-superior Lobule (right) (fig. 58, 4). *Both eyes move upwards and to the right, rotating on their axes.*

This movement resulted from irritation applied to various points on this lobe.

5. Floccular Region (right) (fig. 59, 5).

Rotation of the eyeballs on their antero-posterior axes, sometimes to the right, sometimes to the left, according to the

application of the electrodes on various points in this region, but the situation could not be determined with accuracy.

In the dog, also, I have observed movements of the limbs, nostrils, and ears during irritation of the cerebellum. Owing to the head being fixed, movements, if any, which might be caused were rendered impossible.

Experiments on the cerebellum of the cat led to essentially the same results from stimulation of corresponding regions, as will be seen by the following:—

Electrisation of the Cerebellum of Cats.

Median Lobe.

1. Pyramid (here curved in the form of an S) (fig. 60, 1 *a*, 1 *b*).

a. Right curve.—*Both eyes move to the right.*

b. Left curve.—*Both eyes move to the left.*

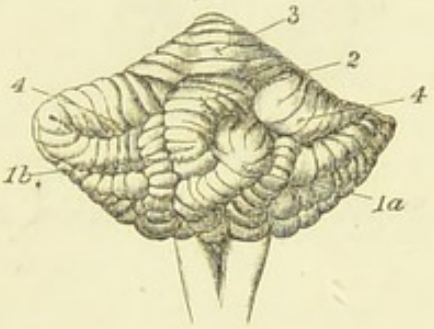


FIG. 60.—Cerebellum of Cat, postero-superior Surface. 1, S-curved pyramid of middle lobe. 2, declive. 3, anterior extremity of median lobe (monticulus). 4, postero-superior lobule.

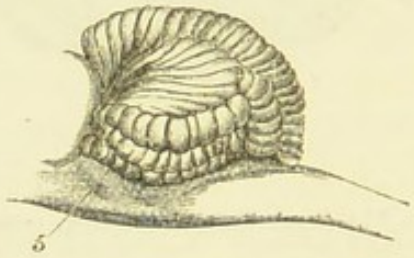


FIG. 61.—Left side of Cerebellum of Cat. 5, floccular region.

2. Upper Vermiform Process.

Posterior Extremity (declive) (fig. 60, 2).

a. Middle.—*Both eyes move downwards.*

b. Left side.—*Both eyes move downwards and to the left.*

c. Right side.—*Both eyes move downwards and to the right.*

Lateral Lobe (fig. 60, 4).

3. Postero-superior Lobule—various points.

Left.—*Both eyes move upward and to the left.*

Right.—*Both eyes move upward and to the right.*

Besides these movements of the eyeballs, it was observed

that on irritation of the left side of the cerebellum the left pupil became contracted, and the left limbs were thrown into action. Movements of the head, if any, were not noted.

Both in the cat and dog the cerebellum is difficult to reach, and, owing to the proximity of large venous sinuses, great and often fatal hæmorrhage results from attempts at complete exposure; hence, I have not succeeded in arriving at trustworthy conclusions in reference to the irritation of other regions.

These results, though incomplete, serve more particularly to indicate the homology of function between the cerebellum of the cat and dog and that of the monkey and rabbit, which were more fully and more frequently explored.

For the purpose of comparison some experiments were made on the cerebellum of pigeons and fishes (carp).

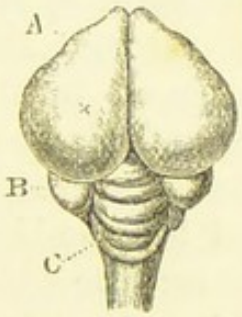


FIG. 62.—Brain of Pigeon. C, the cerebellum.

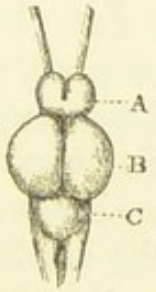


FIG. 63.—Brain of Carp. C, the cerebellum.

§ 11. *Electrisation of the Cerebellum of Pigeons* (fig. 62, C).

Irritation of the cerebellum of pigeons causes no movements of the eyeballs, but, according as the electrodes are applied to the right or left side, the head is jerked backwards and to the same side, and frequently the wing of the same side is flapped and the leg drawn up.

Electrisation of the Cerebellum of Fishes (Carp) (fig. 63, C).

Irritation of the right side causes the eye on the same side to be jerked forwards, the tail to be bent to the right, and the fins spread out. Irritation of the left side causes exactly the same manifestations on the left side, while irritation on the middle of the cerebellum causes the eyes to be jerked for-

wards, the tail to be bent up towards the head, and the fins to be spread out—a state of opisthotonus.

§ 12. The experiments on the cerebellum of mammals receive a remarkable confirmation from, and confer an important significance on, the phenomena which are observed in man when a galvanic current is passed transversely through the skull in the cerebellar region. These phenomena were first described by Purkinje,[1] and more recently they have been very fully investigated by Hitzig.[2] When a galvanic current of moderate intensity is passed through the head by placing the poles of the battery in the mastoid fossæ just behind the ears, the individual experiences a feeling of vertigo, in which the relation of his body to surrounding objects seems to be, or is, actually disturbed; or external objects seem to alter their relation to him. The direction in which the equilibrium is disturbed, or in which external objects seem to move, depends on the direction of the current through the head. When the positive pole, or anode, is placed in the right mastoid fossa, and the negative pole, or kathode, in the left, so that the current passes from right to left, at the moment when the circuit is closed, the head and body suddenly sink towards the anode, while external objects seem to whirl to the left. The direction in which external objects seem to move is compared by Purkinje to the motion of the tire of a wheel, standing parallel to the face, from right to left. When the eyes are closed the appearance of motion is transferred to the individual himself, who feels as if he were suddenly whirled from right to left, or as if the basis of support on the left side had been suddenly withdrawn. The direction is exactly reversed when the positive pole is placed on the left and the negative on the right side; or, while the electrodes maintain their former position, when the circuit is broken.

It has been found by Hitzig that at the moment when the head inclines towards the anode the eyeballs also move in the same direction, and then undergo oscillations, or strain towards the side of the cathode. The ocular deviations are a combination of lateral and rotatory movements.

[1] *Rust's Magazin*, 1827.

[2] *Untersuch. ü. das Gehirn*, p. 198 *et seq.*

In the objective effects of the galvanic current directed through the head in this manner we see, on the side of the anode, essentially the same phenomena as result from the direct application of the electrodes to the same side of the cerebellum; for, as is shown by the foregoing experiments, the predominant direction of the head and eyes is to the same side, with some degree of diagonal or rotatory motion. This gives us strong grounds for attributing the phenomena to irritation of the cerebellum on the side of the anode. And this would agree with the law of galvanic stimulation of the cerebral hemispheres, in which, as Hitzig found, the anode is the more effective. On what this important variation from the usual law of galvanic stimulation of nerve structures depends is not quite clear; but it is probable, as De Watteville [1] has pointed out, in connection with the unipolar excitation of nerves, that the real excitant is the virtual cathode established in the deeper tissues by the application of the anode on the surface. It is in accordance with the law of electrotonus that breaking the circuit reverses the conditions of irritation; hence at the interruption of the current the other half of the cerebellum becomes stimulated, and all the objective phenomena, viz. the inclination of the head and eyes, occur towards the opposite side.

§ 13. But simultaneously with these objective effects there occur certain modifications of consciousness or subjective sensations, which have an important bearing on the true significance of the cerebellar movements. Modifications of consciousness must, however, be regarded as coincident only, and not correlated with cerebellar action as such. The fact that removal of the cerebral hemispheres annihilates consciousness and volition, while it does not affect the function of equilibration, shows that the co-ordination of sensory impressions with special motor adjustments is an independent responsive mechanism. Hence it seems to me a radical error to account for the objective phenomena by any sensations experienced by the individual, such as a *feeling* of vertigo or a *feeling* as if the body were suddenly left unsupported on the one side or the other. The subjective phenomena are only

[1] De Watteville, *L'Electrotonus des Nerfs chez l'Homme*, 1883.

simultaneous accompaniments of the objective, and depend, not on the cerebellum, but on the cerebral hemispheres, just as reflex action may be and often is accompanied by consciousness, though consciousness is not essential to the mechanism itself. Keeping these distinctions in mind, we shall be better able to interpret the relation between the objective and subjective phenomena observed on irritation of the cerebellum.

At the moment when the head and eyes incline to the side of the anode, external objects appear to be whirling to the opposite side. If, on the other hand, the eyes be kept shut, the individual himself feels as if he were being whirled in the same direction as the objects seemed to take when the eyes were kept open. The movement of external objects to the left coincides, as Hitzig has correctly shown, with the ocular movements to the right when the anode is placed in the right mastoid fossa, and the current closed. Now this is precisely the direction in which objects seem to move when the eyes are suddenly deviated to the right. If the right eye is fixed on some object, and the inner side of the eyeball pressed on, the object appears to move to the left. In like manner, if the eyeball is pushed to the left, the object will appear to move to the right; and so it will seem to move up or down, according as the eyeball is pushed downwards or upwards respectively.

Further, if the body be whirled rapidly on a vertical axis in the direction from right to left, external objects will appear to revolve from left to right; an appearance which continues for some time after the rotation has stopped, owing to the persistence of retinal impressions. A feeling of giddiness or insecurity comes on if external objects seem to revolve, and the compensatory action necessary for maintaining the equilibrium is, in the case of rotation to the left, inclination of the head and body to the right side, and deviation of the eyes to the right, in order to keep the objects in view, and thus prevent their passing out of the field of vision. The direction of the eye to the right by voluntary effort, when the body has been whirled from right to left, is sufficient to stop the apparent movement of objects which continues after the rotation has ceased.

From these facts it appears that the effect of irritation of

the right side of the cerebellum is the natural compensatory action which coincides with a feeling of being revolved from right to left; and this is shown very conclusively by the fact that when the eyes are shut the feeling of rotation to the left is the only senstion experienced, and that, too, even when the body is actually inclining to the right side.

The right side of the cerebellum, therefore, co-ordinates the muscular mechanism which prevents the displacement of equilibrium towards the opposite side, and this involves movements of the head, eyes, and limbs on the right side. These are the actual results of the direct application of the electrical stimulus to the cerebellum itself. In like manner, the movements which result from irritation of the anterior part of the middle lobe of the cerebellum, viz. the backward movement of the head and extension of the trunk and limbs, together with the upward movement of the eyes, are to be regarded as the natural compensatory efforts to counteract a seeming rotation forward on a horizontal axis. We may suppose, therefore, that the subjective side of these objective phenomena is a feeling of being revolved like a wheel from behind forwards on a horizontal axis. Similarly the forward movements of the head and downward direction of the eyes, resulting from irritation of the posterior part of the median lobe, are the compensatory or antagonistic actions to counteract a disturbance of the equilibrium in the opposite direction, i.e. from before backwards. Hence we may suppose that irritation of this part coincides with the sensation of rotation like a wheel on a horizontal axis from before backwards.

The cerebellum would, therefore, seem to be a complex arrangement of individually differentiated centres, which in associated action regulate the various muscular adjustments necessary to maintain equilibrium and steadiness of the body; each tendency to the displacement of the equilibrium round a horizontal, vertical, or intermediate axis acting as a stimulus to the special centre which calls into play the antagonistic or compensatory action.

We should, therefore, expect to find that a lesion which annihilates the functional activity of any of the individual cerebellar centres should manifest itself in a tendency to the

overthrow of the balance in the direction naturally opposed by this centre. This also is in accordance with the facts of experiment. We have seen that stimulation of the anterior part of the middle lobe excites the muscular combinations which would counteract a tendency to fall forwards. Hence destruction of this part shows itself in a tendency to fall forwards. In this we see both the negative effect caused by the removal of the one centre, and the positive effect exerted by the unopposed and antagonistic centres.

In like manner, stimulation of the posterior part of the middle lobe calls into play the muscular adjustments necessary to counteract a backward displacement of the equilibrium; and hence, as we have seen, destruction of this region manifests itself in a tendency to fall backwards.

The lateral lobes of the cerebellum contain centres for complex adjustments against lateral, combined with diagonal and rotatory displacements to the opposite side; and hence, as has been found by experiment, lesions of the lateral lobes exhibit themselves in disturbances of the equilibrium, either laterally, to the side opposite the lesion, or as the resultant of lateral and rotatory displacement in rolling over to the side of lesion. The effects of lesion of the lateral lobes may therefore vary—a fact which may account for some of the discrepancies among the results obtained by different experimenters.

§ 14. Every form of active muscular exertion necessitates the simultaneous co-operation of an immense assemblage of synergic movements throughout the body to secure steadiness and maintain the general equilibrium; and on the hypothesis that the cerebellum is the centre of these unconscious adjustments we should expect the cerebellum to be developed in proportion to the variety and complexity of the motor activities of which the animal is capable. The facts of comparative anatomy and development are entirely in harmony with this hypothesis. In the reptilia and amphibia, whose movements are grovelling and sluggish, or of the simplest combination, the cerebellum is of the most rudimentary character; while in mammals it is richly laminated, and the lateral lobes highly developed in proportion to the motor capabilities represented in the motor zone of the cerebral hemispheres.

If we compare the relative development of the cerebellum in the several orders of the same class of animals we find it highest in those which have the most active and varied motor capacities, irrespective of the grade of organisation otherwise ;[1] and the cerebellum of the adult is, relatively to the cerebrum, much more highly developed than that of the new-born infant —a relation which evidently coincides with the growth and development of the muscular system.

§ 15. The mechanism of cerebellar co-ordination is essentially independent of consciousness and volition, and is an example of responsive or æsthetiko-kinetic action. But while we may theoretically in all animals, and practically in many, abolish consciousness and volition by removal of the cerebral hemispheres, and still leave the mechanism of equilibration intact, yet in the normal state cerebellar activity is associated with that of the hemispheres ; an association which serves to explain many of the facts which might seem to oppose the view we have taken of the functions of the cerebellum as a whole and of its individual parts.

The displacement of equilibrium in any direction not only

[1] 'If, on the other hand, we compare the cyclostome and plagiostome cartilaginous fishes, in reference to their modes and powers of locomotion, we shall find a contrast which directly accords with that in their cerebellar development. The myxine commonly passes its life as the internal parasite of some higher organised fish ; the lamprey adheres by its suctorial mouth to a stone, and seldom moves far from its place : neither fish possesses pectoral or ventral fins. The shark, on the contrary, unaided by an air-bladder, sustains itself at the surface of the sea by vigorous muscular exertion of well-developed pectoral and caudal fins, soars, as it were, in the upper regions of the atmosphere, is proverbial for the rapidity of its course, and subsists, like the eagle, by pursuing and devouring a living prey; it is the fish in which the instruments of voluntary motion are best developed, and in which the cerebellum presents its largest size and most complex structure. And this structure cannot be the mere concomitant of a general advance of the organisation to a higher type, for the sluggish rays that grovel at the bottom, though they copulate, and have in most other respects the same grade and type of structure as the more active squaloid plagiostomes, yet have a much smaller cerebellum, with a mere crucial indentation instead of transverse laminæ. . . . Finally, amongst the normal osseous fishes, the largest and highest organised cerebellum has been found in the tunny, whose muscular system approaches, in some of its physical characters, most nearly to that of the warm-blooded classes.'—Owen, *Comparative Anatomy and Physiology of the Vertebrates*, vol. i. p. 287 *et seq.*

calls into play by reflex or responsive action the compensatory motor adjustments, but also induces conscious or voluntary efforts of a similar antagonistic or compensatory nature. Thus a tendency to fall forwards, while reflexly calling into action the muscular combinations which pull the body backwards, may also excite consciousness and cause voluntary effort in the same direction. The same muscular adjustments which are capable of being effected by the cerebellum are also under the control of the will, and may be carried out by the cerebral hemispheres independently of the cerebellum.

Hence it is that lesions of the cerebellum, while interfering with the mechanical adjustments against disturbance of the bodily equilibrium, do not cause paralysis of voluntary motion of the muscles which are concerned in these actions. This is an exceedingly important fact, which, though disputed by some, seems to be established experimentally beyond all question. During the wildest reeling and tumbling of pigeons and other animals, in which the cerebellum has been destroyed, there is no sign of muscular paralysis or diminution of the energy of muscular contractions; and I have carefully investigated the condition of the muscular system in monkeys, in which lesion of the cerebellum had caused such disorders of the equilibrium that locomotion was impossible, and have found that voluntary movements of the head, trunk, and limbs were freely carried out in the recumbent position. The facts on which the statement has been founded that lesions of the cerebellum produce paralysis of motion on the opposite side of the body are susceptible of quite a different interpretation. It has been observed that tumours, or apoplectic extravasations into one half of the cerebellum, frequently coincide with hemiplegia of the opposite side of the body. But in these cases, as Vulpian has rightly indicated, the hemiplegia is not the result of the cerebellar lesion as such, but of compression or interference with the subjacent tracts of the pons and medulla. As these decussate in the medulla oblongata, the effect of compression by a tumour of the lateral lobe of the cerebellum is paralysis on the opposite side of the body.

Lesions of the cerebellum which do not exert such an influence on the subjacent tracts do not cause hemiplegia on

the opposite side. The lateral lobe co-ordinates muscular adjustments mainly on the same side of the body, but as these are called into action by reflex stimulation, it is only this form of co-ordination which is suspended by lesions of the cerebellum; a condition, however, which is essentially distinct from paralysis of voluntary motion. The effect, whatever name it may be best designated by, is direct and not crossed.

In terming the effect of cerebellar lesion a paralysis of reflex adjustment I do not thereby imply a paralysis of reflex action. This, which would result from spinal lesion, must necessarily coincide with paralysis of voluntary motion, as the path from the hemispheres would thereby be interrupted. What is implied is that the same combinations of muscular action which are co-ordinated in the cerebellum for the maintenance of the equilibrium are capable of being called into voluntary action by the cerebral hemispheres. Hence, though lesions of the cerebellum destroy the self-adjusting co-ordination of muscular combinations necessary to maintain the equilibrium, they do not cause paralysis of voluntary motion in the same muscles. So, conversely, by removal of the cerebral hemispheres we cause paralysis of voluntary motion, but do not affect the independent mechanism of cerebellar co-ordination. When we make this necessary distinction we are enabled to understand how limited lesions of the cerebellum may produce only transient effects, and how even complete destruction of the cerebellum may ultimately be recovered from.

§ 16. The disturbance of equilibrium is always most marked immediately after the infliction of injury to the cerebellum. This, which has been by many looked upon as a sign of irritation, is to be accounted for by the sudden derangement of the self-adjusting mechanism on which the maintenance of the equilibrium mainly depends. As, however, the animal may supplement the loss of this mechanism by conscious effort, in process of time it acquires the power of voluntary adaptation, and thus is enabled to maintain its equilibrium, though perhaps with a less degree of security than before.

The more extensive the lesion, the greater the disturbance of the mechanism, and the greater the difficulty of effecting

through conscious effort all the muscular adjustments necessary to maintain the balance. The disturbances of equilibrium are therefore of a more enduring character, and it is only by a long process of training that volitional acquisition can replace a mechanism essentially independent of consciousness. Even should this point be reached, the constant attention necessary to preserve steadiness of movement, and prevent displacement of equilibrium, would be a heavy strain on the animal's powers; and it would be in accordance with this condition that prolonged or varied muscular exertion should cause great apparent exhaustion. Such, in fact, was observed by Weir Mitchell[1] to be the case in some pigeons in which he had inflicted considerable injuries on the cerebellum. In one of these, four months after the operation, no other abnormality could be detected except that when pursued about the room it gave out sooner than its fellows, and often quite suddenly. The last sign of awkwardness was a certain want of power to direct its beak.

A similar feebleness and incapacity for prolonged exertion was observed by Luciani in the dogs which have been referred to above (p. 178).

But these facts do not necessitate the hypothesis originally advocated by Luys, and supported by Weir Mitchell and Luciani, that the cerebellum is a reservoir of energy for the reinforcement of movements throughout the economy. There is no diminution in the force of muscular contractions after cerebellar lesions. By sparing higher centres the cerebellum may in one sense be regarded as a source of energy, but the real cause of the apparent fatigue exhibited by animals after cerebellar lesions is the fact that all their motor adjustments, formerly easy and automatic, are now performed under a laborious sense of strained attention and conscious effort. The cerebral hemispheres have to perform the work formerly done by the cerebellum, and there can be little doubt that the removal also of the cerebral hemispheres would render the animal absolutely helpless. This is in a measure verified by the condition of Luciani's dog in which the sigmoid gyri were also destroyed (p. 179).

[1] *Amer. Journ. Med. Sci.*, 1869.

A similar mode of explanation is applicable to those cases of atrophy or disease of the cerebellum which have run a latent, or almost latent, course during life. A congenital defect, or slowly progressive lesion, would be the most favourable condition for the supplementation by conscious effort of a self-adaptive mechanism which is more or less entirely wanting, or gradually undergoing degeneration. But congenital defects or lesions in early life have been found associated with very tardy acquisition of stability of locomotion, and it is questionable whether in man perfect substitution is possible, a want of precision and energy, and a continual tendency to reel or fall being generally observable.

§ 17. In a previous chapter (Chapter IV.) the maintenance of equilibrium was shown to be an example of adaptive or responsive action depending on the co-ordination, in some central organ, of certain afferent impressions with the requisite motor adjustments. The afferent factors of this mechanism were found to be mainly of three kinds; viz. tactile, visual, and labyrinthine impressions; and it was seen that marked disturbances of equilibrium resulted from perversion or interference with any part of this afferent system. The foregoing experiments on the cerebellum justify the conclusion that the cerebellum is the great central organ of this co-ordination. This view is further confirmed by a comparison of the disturbances of equilibrium, consequent on lesions of the cerebellum, with those resulting from morbid affections of the afferent apparatus, as well as by a consideration of the anatomical relations of the cerebellum itself.

The afferent impressions conveyed to and calling forth the action of the cerebellar centres were regarded as physical in contradistinction to psychical modifications; and though under normal conditions these may be coincident with modifications of consciousness, consciousness is neither essential nor is it a correlative of cerebellar action as such.

We should not expect, therefore, that lesions of the cerebellum would cause any affection or paralysis of either tactile, visual, or auditory sensation, properly so called, even though a direct connection of these nerves with the cerebellum should be anatomically demonstrated.

The cerebellum was regarded by many of the older writers as the seat of common sensibility. This opinion was founded chiefly on the continuity of the posterior columns of the spinal cord with the restiform tracts or inferior peduncles of the cerebellum. That the restiform bodies are mediately related with the posterior columns, through the olivary bodies, has been established by the researches of Meynert and other anatomists, the relation being mainly cross, i.e. the restiform body on the one side being related to the opposite posterior column.

The posterior columns being regarded as the path of common or tactile sensation, the opinion that the cerebellum was the seat of common sensibility seemed well founded. But we have seen that the more recent investigations into the sensory paths of the spinal cord do not support this view of the functions of the posterior columns; for tactile sensibility is certainly not abolished by section of these tracts (see Chap. II. § 6). Brown-Séquard has also shown by direct experiment that section of the restiform bodies does not cause loss of tactile sensation. These facts, in conjunction with the results of experimental lesions and disease of the cerebellum, afford overwhelming evidence against the view that the cerebellum is the seat of common sensation. Neither Flourens, Vulpian, Luciani, nor other recent experimenters have ever observed cutaneous anæsthesia in animals deprived of their cerebellum, nor have I in monkeys or human beings observed any indications of cutaneous anæsthesia after extensive lesions or disease of this organ.

Lussana [1] endeavours to show that cerebellar inco-ordination is due to loss of the muscular sense. But this is a pure assumption, and he supplies no tangible evidence of the actual impairment of this so-called sense. It is extremely difficult to test the muscular sense in the lower animals, but I have observed monkeys which, owing to lesion of the cerebellum, were unable to maintain their equilibrium handle and grasp objects with as great precision and firmness as before. The best evidence on this head is furnished by the facts of disease

[1] 'Sur les Fonctions du Cervelet,' *Journ. de la Physiologie*, tome v. 1862, and tome vi. 1863.

in man, and these prove beyond all doubt that the muscular sense may be entirely unaffected in cases in which the characteristic titubation is most pronounced.

These considerations, however, though sufficient to dispose of the view that sensation proper in any of its forms is affected by cerebellar lesions, by no means oppose the view that through the restiform bodies and their connections with the posterior columns of the spinal cord the cerebellum is brought into relation with certain centripetal impressions, which with others serve to call forth the muscular adjustments requisite for equilibration. As a matter of fact, injuries of the restiform tracts induce the most turbulent disorders, similar to those caused by lesion of the semicircular canals.[1] Whether this is due to lesion of the root of the vestibular nerve which joins the restiform tract, or to injury of other afferent tracts, or to both, is not easy to determine. But the experiments of Bechterew[2] on the olivary bodies show that lesions of these structures induce also disturbances of equilibrium, with rolling or *manège*, forced movements, and deviation of the optic axes similar to those caused by lesion of the middle cerebellar peduncles. These facts render it probable that it is through the medium of the olivary bodies that the impressions conveyed by the posterior columns of the cord ascend to the cerebellum through the restiform tracts, and that it is the interruption of these connections which lead to the disorders of equilibrium which ensue. The restiform bodies are also related, as has been already described (Chapter I. § 5) to the direct cerebellar tracts derived from the cells of Clarke's vesicular column, and the portion of the spinal roots which enter them. What is the true function of these centripetal tracts has not been definitely determined, and we can only speculate on the subject (see below, p. 218). But that it is through the restiform tracts that the tactile impressions are conveyed, which form such an important factor in the consensus of afferent impressions which excite and regulate cerebellar co-ordination, seems to be fairly well established.

[1] Laborde, *Comptes Rendus de la Société de Biologie*, June 1882.

[2] *Ueber den Olivenkörper der Med. Oblong. Wratsch*, 1882, No. 35. Abstract in *Neurolog. Centralbl.*, Dec. 1, 1882.

§ 18. Another important factor in the mechanism is the connection between the auditory nerve, or a portion of it, and the cerebellum. A division of the auditory nerve, the anterior, which is in especial relation with the ampullæ of the semicircular canals, appears to ascend directly into the cerebellum by the restiform tract, and is considered by some anatomists also to have connections with a nucleus (Deiter's nucleus) situated in the restiform tract, and through this indirectly with the cerebellum. But, as has been seen, this connection cannot be looked upon as at all satisfactorily established. The central connections of the auditory nerve are still obscure, but there can be no doubt that certain of the fibres ascend directly to the cerebrum without entering the cerebellum. Meynert's view, that the whole of the roots of the auditory nerve pass into the cerebellum in the first instance, and only indirectly into the cerebrum, possibly through the valve of Vieussens or superior peduncles, is clearly untenable. Lesions of the cerebellum do not impair the sense of hearing in animals, nor do diseases of the cerebellum in man cause deafness, except in such cases as lead to direct implication, by pressure or the like, on the auditory nerves themselves.

We have already seen, however, the enormous influence exercised by the semicircular canals on the faculty of equilibration, and we have the anatomical foundation of this relation in the connection which exists between the labyrinth and the cerebellum. There is further a remarkable and significant similarity between lesion of the individual semicircular canals and injury of certain regions of the cerebellum, and also between direct irritation of the canals and electrical irritation of different portions of the cerebellar cortex.

It has been seen that section of the superior vertical canals causes displacement of equilibrium forwards, or diagonally round a horizontal axis—an effect which corresponds with lesion of the anterior part of the middle lobe of the cerebellum. Section of the posterior vertical canals causes a tendency to fall backwards or describe a somersault backwards round a horizontal axis—an effect which corresponds with injury of the posterior part of the median lobe. Section of the horizontal canals causes lateral or rotatory displacements

round a vertical axis—an effect which corresponds with injury of the lateral lobes.

The experiments of Mach and Crum-Brown already referred to (Chapter IV. § 14) show that rotation backwards round a horizontal axis is calculated to cause irritation of the nerve-endings in the ampullæ of the superior vertical canals, perhaps by increased tension, or otolithic vibration, in these relatively to that in the opposed posterior vertical canals. Rotation forwards round a horizontal axis causes a reversal of these conditions, leading to increased irritation of the posterior vertical as compared with the superior vertical canals. Rotation round a vertical axis causes increased tension or irritation of the ampullary nerves of the horizontal canal on the side from which the rotation takes place.

From previous considerations we may assume that the ampullary irritation acts as the stimulus to the motor adjustments calculated to oppose the displacement of the equilibrium in the direction which coincides with this irritation. Assuming the seat of irritation to be correctly indicated by Crum-Brown, we should regard the superior vertical canal as the afferent of the posterior cerebellar centres, the posterior vertical canal as the afferent of the anterior cerebellar centres, and the horizontal canal as the afferent of the corresponding lateral centres. If these conclusions are well founded, we should expect that carefully localised irritation of the several ampullæ should excite movements of the eyes, head, and trunk, harmonising with those resulting from direct irritation of the correlated cerebellar regions.

§ 19. As a matter of fact, the experiments of Cyon, Högyes, and others on animals, and the results of irritation of the labyrinth in man, strongly confirm the above hypothesis both generally and in detail. Localised irritation of the individual canals is, however, surrounded with numerous difficulties, and especially electrical irritation, on account of the complications induced by extrapolar diffusion. But apart from the possible complications caused by the operative procedure, no valid objection can be made against the experiments of Cyon and Högyes, in which the canals were irritated by the slight touch of as ponge or a bristle. In a memoir presented to the

Académie des Sciences in 1877 [1] Cyon described a series of ocular movements and oscillations which he observed on mechanical irritation of the semicircular canals in rabbits. The great feature of these ocular movements was that the direction was determined by the canal irritated. 'Each semicircular canal has a special influence on the ocular movements. Excitation of the horizontal canal in the rabbit produces a rotation of the eye on the same side in such a manner that the pupil becomes directed backwards and downwards; excitation of the posterior vertical canal causes a deviation of the eye so that the pupil looks forwards and slightly upwards; while irritation of the superior vertical canal causes a deviation backwards and downwards. The excitation of each canal always causes movements of both eyes, but the movements of the opposite eye are contrary to those of the side irritated. The pupil contracts on the side irritated and becomes dilated on the opposite.

Cyon, however, in his thesis [2] makes some modification of his statements as to the direction of the ocular movements, particularly as regards those depending on irritation of the horizontal and posterior vertical canals. Irritation of the horizontal canal, he says, causes the globe to be directed forwards and downwards; of the posterior vertical canal, backwards and upwards; and of the superior vertical canal, backwards and downwards. In the other eye the direction is contrary, viz. backwards and upwards, forwards and downwards, and forwards and upwards, on irritation of the horizontal, posterior, and superior vertical canal respectively. This discrepancy is doubtless due to the fact that the nystagmus which comes on after the first deviation, which is almost tetanic in character, is apt to mix itself up with the direct effects of irritation, and to reverse the really primary movement. The results first obtained by Cyon seem to me more in accordance with other facts than his later ones.

Högyes [3] finds that touching the horizontal canal or ampulla, causes the eyes to turn to the same side, and induces nystagmus in the same plane. With the nystagmus are

[1] 'Les Organes Périphériques du Sens de l'Espace,' *Comptes Rendus*, 1877.
[2] Thèse: *Sur les Fonctions des Canaux Semicirculaires*, 1878. [3] *Op. cit.*

associated also movements of the head and body. Irritation of the left vestibular nerve generally causes the eye of the same side to move upwards and outwards, and rotate inwards; while the opposite eye moves downwards and inwards, and rotates outwards. Irritation of the right vestibular nerve exactly reverses these movements in the two eyes. Spamer's experiments with faradic and galvanic stimulation possess so little uniformity that the methods must be regarded as unsatisfactory.

Of a similar nature to the irritation induced by actual touching of the canals is that observed in man by the injection of air or liquids into the ear in cases of rupture of the membrana tympani. In a case of this kind Lucae [1] observed that injection into the left ear caused the eyes to turn to the left, accompanied by a subjective appearance of objects moving suddenly to the right and a feeling of vertigo; while injection into the right ear exactly reversed the phenomena.

§ 20. The results of direct irritation of the semicircular canals, though in some respects in need of revision, and perhaps modification, are essentially similar to those of direct irritation of the cerebellum itself in different regions. The predominant direction of the ocular and other movements is in some axis inclining to the side of irritation. Under normal conditions there would appear to be a balance of opposing forces, so that overaction in any one direction is calculated to call into play the antagonistic adjustment. Hence the primary ocular deviation is always followed by a reflux oscillation in the reverse direction. Should, however, the one limb of the mechanism act in excess of the other, either as the result of abnormal irritation of the ampulla or the correlated cerebellar centre, or as the result of destructive lesion of the same parts, the balance will be overthrown in the direction of the predominant or unopposed force. But the direction of the overthrow in cases of irritation ought to be exactly the reverse of that in cases where the lesion is purely destructive. In experimental lesions both factors may be at work and not easily separable, but we need not assume, as some have done, that the effects of lesion of the semicircular canals are only phe-

[1] *Archiv f. Ohrenheilkunde*, Bd. vii. Heft iv. 1881.

nomena of irritation. The tendency in simple and uncomplicated irritation seems to be overthrow of the balance towards the side of irritation, or in some axis inclining in this direction. This frequently occurs in Menière's disease, in which there seems to occur paroxysmal irritation of the semicircular canals, accompanied by hissing or ringing in the affected ear and a distressing sense of vertigo. But the direction in which the balance is overthrown is not always towards the side of irritation, for I have observed it in several patients clearly towards the opposite side. This is probably due to over-compensation. The sense of falling to one side causes active volitional effort on the part of the individual, so that he falls in reality towards the opposite side. It is the presence of the hemispheres, and the intervention of conscious and volitional efforts, which complicate all the properly reflex phenomena of cerebellar adjustments. Hence it is that irritation of one side of the cerebellum causes the feeling of rotation towards, or loss of support on the other side, because, as the action which is called forth is in reality the adjustment to counteract such displacement, the two become indissolubly associated in consciousness, and the one effect invariably calls up the other. The feeling of loss of support on the opposite side of the body may be regarded as analogous to the apparent vanishing of objects in the same direction. When the various factors concerned in the mechanism of equilibration appear out of harmony, or contradictory to each other, a distressing sense of insecurity and faintness is the inevitable result. This is merely the psychical side of motor disturbances, which, apart from the cerebral hemispheres, would occur without any such accompaniments.

§ 21. While the anatomical as well as the physiological connection of the cerebellum with the auditory nerve is sufficiently clear, we cannot say the same of the relation between the cerebellum and the eyes. That destruction of the cerebellum does not affect the sense of sight is amply demonstrated by the experiments of Flourens and other physiologists. Animals in which the cerebellum has been destroyed evidently see and appreciate threats, and endeavour to escape, but their efforts to do so only end in turbulent confusion. The sense

of sight is a function of the cerebral hemispheres. Blindness does not occur in cases of atrophy of the cerebellum in man, but it is not an infrequent result of tumours situated in the cerebellum, as elsewhere. Loss of vision from intracranial tumours is caused by the secondary changes induced in the optic nerves, purely by indirect action, and has no special relation to the situation of the tumour. But, though the cerebellum is not essential to the sense of sight, yet that it has intimate relations with the optic and oculo-motor nerves is shown by the importance of visual impressions in the mechanism of equilibration, and by the relation between oculo-motor and general motor adjustments, which has been demonstrated by the above recorded experiments. We have yet much to learn respecting the constitution and connections of the superior cerebellar peduncles and valve of Vieussens, and respecting the relations between the red nuclei and the optic and oculo-motor nerves. That we have in these anatomical connections between the cerebellum and the eyes is, on many grounds, highly probable. The superior cerebellar peduncles, as has been seen (Chapter I. § 7), decussate into the red nuclei, but their further relations are highly obscure. A case of great importance in this relation has recently been carefully examined and put on record by Mendel.[1] In this case there was, apparently in consequence of primary lesion (a hæmorrhagic focus) in the pulvinar of the left optic thalamus, atrophy of the left red nucleus, and a tract of secondary degeneration in the right superior cerebellar peduncle, traceable as far as the nucleus dentatus. Mendel suggests, with great probability, that this may be the medium of communication of optical impressions with the centres of equilibration.

By the decussation of the superior peduncles the optic tracts would thus be in cross relation with the cerebellar hemispheres, and, owing to the decussation in the optic chiasma, the eyes would be mainly in direct relation with them. This would be in harmony with the fact observed on electrical irritation of the cerebellum, viz. that the pupil on the same side became contracted.

Lesions of the superior peduncles of the cerebellum, as

[1] 'Secondäre Degeneration im Bindearm,' *Neurolog. Centralb.*, No. 11, 1882.

well as of the structures with which they are in relation, produce marked disturbances of equilibrium, for such disturbances must necessarily ensue upon lesions of any part of the mechanism, whether central, afferent, or efferent. Lesions of the optic lobes, or of the connections between the optic or oculo-motor nerves, would naturally have this effect. To interruption of the connections of the superior peduncles, or to direct injury of the oculo-motor nuclei, or both, are doubtless due the very marked disorders of equilibrium observed by Bechterew[1] in connection with lesions of the walls of the third ventricle and neighbourhood of the aqueduct of Sylvius; disorders which have all the characters of those which result from lesions of the semicircular canals or olivary bodies of the medulla oblongata.

§ 22. Whether in the inferior and superior peduncles there are efferent as well as afferent cerebellar tracts is a question on which we have little or no definite information. I have found both in rabbits and in monkeys that electrical irritation of the restiform tract causes movements of the head, trunk, and limbs, with a tendency to pleurosthotonus on the same side. These might be merely reflex phenomena, but the fact that, after deep transverse section, irritation of the part below the cut produces precisely the same action as before, while irritation above the cut is absolutely negative, rather favours the idea that the restiform body may contain efferent motor tracts. But the question is one which requires further investigation. Respecting the superior peduncles it is stated by Albertoni and Michieli[2] that electrical irritation or puncture causes pleurosthotonus towards the side opposite the irritation. They are disposed to regard these phenomena as direct rather than reflex on the ground that they occur when the sensibility has been entirely exhausted.

[1] 'Die Function der centralen grauen Substanz des dritten Hirnventrikels,' Pflüger's *Archiv f. Physiologie*, Bd. xxxi. July 1883.—The hypothesis advanced by Bechterew, that the grey matter of the walls of the third ventricle acts as a peripheral organ to the centres of equilibration—similar to the semicircular canals—impressions in which are conditioned by varying degrees of pressure of the contained cerebro-spinal fluid caused by movements of the head and of the eyeballs, has at least the merit of originality.

[2] 'Sui Centri Cerebrali di Movimento,' *Lo Sperimentale*, 1876.

§ 23. The middle peduncles of the cerebellum form the great medium of connection between the lateral lobes of the cerebellum and the pyramidal motor tracts. These peduncles, as has been shown by Meynert, decussate in the pons and enter into intimate relations with the opposite pyramidal tracts through the cells of the nucleus pontis. A direct connection between the peduncular and pyramidal tracts is doubtful. The cross relations between the peduncular and pyramidal tracts in the pons bring the lateral lobes of the cerebellum in relation with the motor tracts on the same side, owing to the decussation of the pyramidal tracts at the lower aspect of the medulla oblongata. These anatomical facts are in harmony with the effects of electrical irritation of the cerebellum, by which, as has been seen, movements are excited on the same side of the body. The functional relationship to the two sides of the body is therefore cross in the case of the cerebral hemispheres and direct in the case of the cerebellar lobes; and thus each cerebral hemisphere acts in combination with the opposite cerebellar lobe. That this is so, and that the cerebellum acts in subordination to the cerebrum, is shown by the fact that in many cases of long-standing disease of one cerebral hemisphere, atrophy ensues in the opposite lobe of the cerebellum. In a case of this kind which I have recorded[1] there was marked atrophy of the right lobe of the cerebellum consecutive to destruction of the anterior or motor region of the left hemisphere (figs. 64 and 65).

The pyramidal tract of the left side had undergone secondary degeneration, and, with it, the right middle peduncle and right lobe of the cerebellum had become greatly reduced.

An examination of the cortex of the right lobe of the cerebellum proved also that this had undergone extreme degenera-

[1] 'Brain of a Criminal Lunatic,' *Brain*, April 1882.—The patient was a woman who, after the age of thirty, became suddenly aphasic and hemiplegic on the right side. She became insane, murdered her two children, and was committed to Broadmoor Asylum, where she died twelve years after the occurrence of the paralysis. The whole of the cortex in the region indicated in the figure, together with the corpus striatum, had entirely disappeared, and been converted into a cyst full of fluid. For further details reference may be made to the original paper cited.

tion, and that the cells of Purkinje had in many parts entirely disappeared (fig. 66, B).

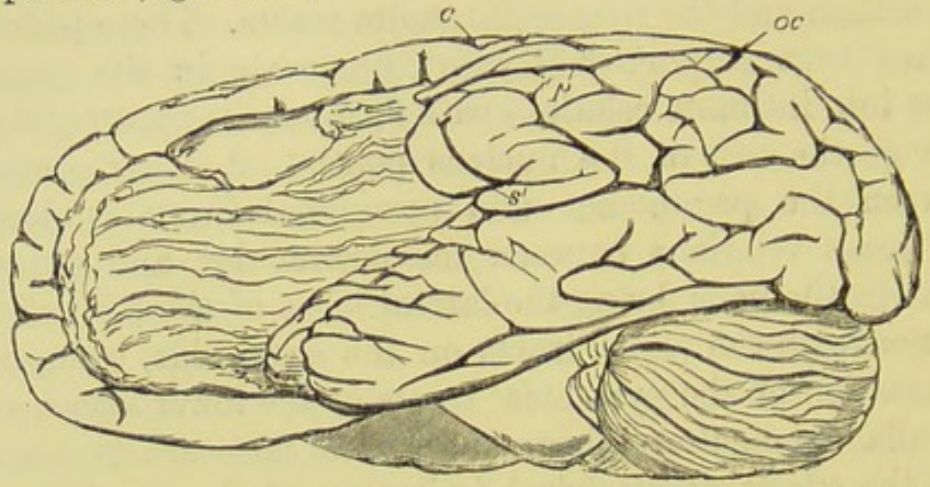


FIG. 64.—Side view of Brain, in which the anterior half of the left hemisphere had become atrophied in consequence of disease. *c*, upper extremity of the fissure of Rolando of right hemisphere. *p*, intraparietal fissure. *s'*. extremity of horizontal limb of fissure of Sylvius. *oc*, parieto-occipital fissure.

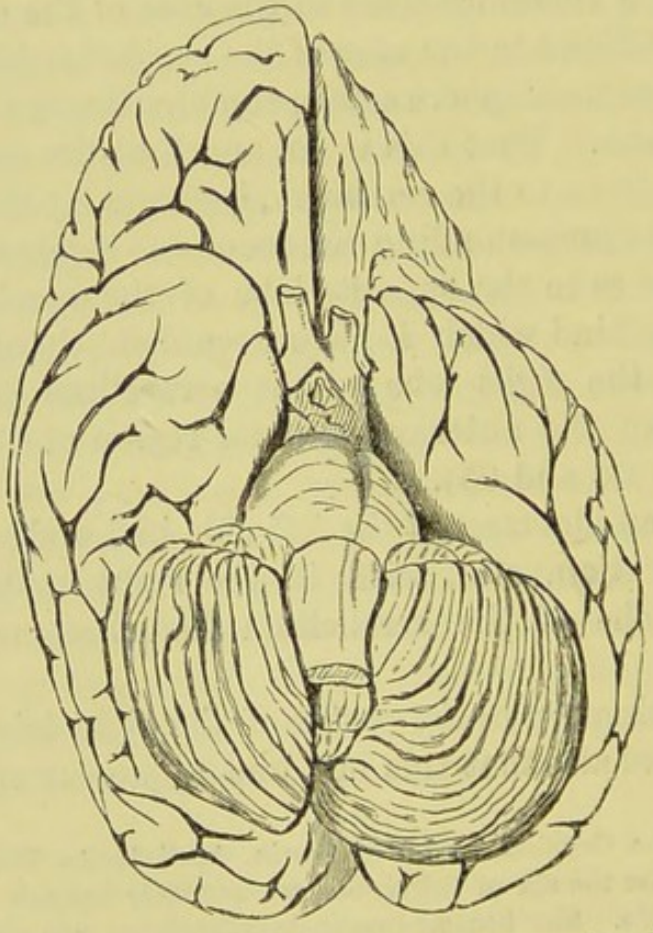


FIG. 65.—Under Surface of same Brain (Fig. 64), showing Atrophy of the right lobe of the Cerebellum.

§ 24. It is a question whether, along with tactile or common sensory, visual, and labyrinthine impressions, other sensory

impressions are correlated in the cerebellum with the motor adjustments necessary for stability and equilibration. On a former occasion [1] I ventured to suggest that possibly visceral

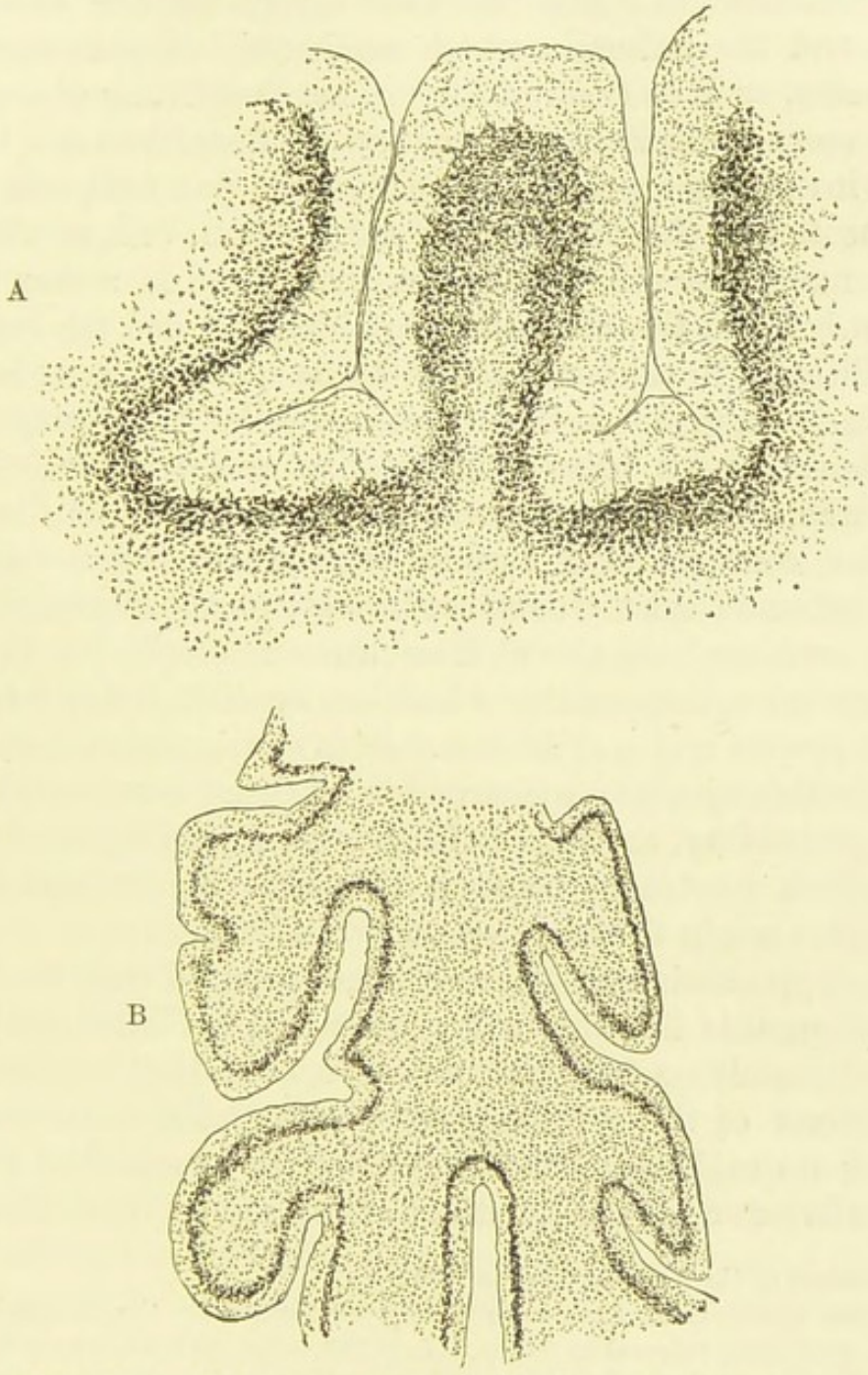


FIG. 66.—A, Section of a Leaflet of the left lobe of the Cerebellum (normal). B, Section of a Leaflet of the right lobe, showing disappearance of Purkinje's cells and atrophy of the granular layer. (From preparations and drawings by J. A. Scott.)

or organic sensory impressions were represented in the cerebellum, mainly on the ground of the very intimate mutual

[1] First edition of this work, § 26.

reactions between states of the viscera and the exercise of equilibration. I instanced among other things the very pronounced disturbances of equilibrium and vertiginous sensations which are experienced in connection with certain visceral derangements, and the influence which mechanical displacement of the viscera, such as occurs in the rising and falling of a vessel at sea, seems to have in the production of sea-sickness. The almost invariable expression of vertigo in a peculiarly distressing sensation in the region of the epigastrium, with or without actual nausea or vomiting, shows that there is a very close relation between the centres of equilibration and the organic sensibilities. In connection with these speculations it is permissible to suggest that the direct cerebellar tracts may form the afferent paths between the viscera and the cerebellum. These tracts, as has been seen, connect the cells of Clarke's vesicular columns with certain cortical cerebellar regions. These columns exist almost exclusively in the dorsal region of the cord, and are absent from those regions—the lumbar and cervical enlargements—which are specially related to the animal powers and sensibilities. Ross's [1] suggestion that they are therefore specially concerned in visceral innervation has much probability, and this is further supported by the homology which he traces between Clarke's columns and those which give origin to the accessorio-vagus.[2]

The hypothesis that the cerebellum presides over the functions of organic life was first propounded by Willis, and was founded mainly on false anatomical views as to the origin and connections of the pneumogastric nerve. There is, indeed, little or no evidence that the cerebellum is essential to the due performance of the functions of organic or vegetative life.

[1] *Diseases of the Nervous System*, 1881.

[2] These speculations have been amply confirmed by the researches of Gaskell, previously referred to (Chap. III., p. 103, note), which have shown that the appearance of the cells of Clarke's vesicular column coincides with that of the fine medullated nerves which constitute the visceral spinal system. 'Although as yet the fine medullated fibres which constitute the rami viscerales have not been directly traced into the cells of the columnæ vesiculares, the connection of these fibres with this column of cells is, to my mind, proved conclusively by the fact that **the cells of Clarke's column are confined to those regions of the central nervous system which give origin to the rami viscerales.**'—Gaskell, *op. cit.* p. 56.

Willis's hypothesis has been, however, revived by Luciani [1] on what appear to be most slender and unsatisfactory grounds. In one of the dogs before mentioned (p. 178), from which he had removed the greater portion of the cerebellum, general malnutrition and marasmus occurred in the later months of its survival. But as the animal had attained a state of good health and nutrition after the primary effects of the operation had subsided, and as coincident with the marasmus and malnutrition there were signs of purulent otitis and catarrhal conjunctivitis, it is much more likely that the marasmus was caused by the suppuration and its attendant constitutional disturbance, than that any of these effects depended on the destruction of the cerebellum as such. The condition of the second dog at the end of a much longer period of survival is quite sufficient to dispose of Luciani's hypothesis, founded as it was on the results only of the first experiment. In the second animal the state as regards nutrition was altogether excellent. The committee of investigation reported: 'The weight was 4·900 grams; the body was well nourished, and the adipose tissue was abundant.'

Notwithstanding the large amount of research that has been expended on the cerebellum there are many points in its anatomy and physiology on which we are as yet devoid of precise information, and the opinion of Vulpian, writing in 1866—'that the problem of the functions of the cerebellum is still far from being definitely solved'—will still apply to the present state of our knowledge. But, though the exact formula of cerebellar function may yet have to be found, the effects of injury and disease of this organ have been fairly well ascertained; and these show that the functions of the cerebellum are outside the sphere of mind proper, as expressed in sensation, emotion, volition, and intellect.

[1] *Fisiologia del Cervelletto*, 1884.

CHAPTER VII.

FUNCTIONS OF THE CEREBRUM.

Introductory—Method of Investigation.

§ 1. In the preceding chapters we have seen that, notwithstanding the complete removal of the cerebral hemispheres, animals, in proportion to their lowness in the scale, still remain capable of a great variety of most complex and adaptive forms of activity, little if at all differing in character from those prompted by intelligence. On more detailed investigation of these forms of activity, however, the conclusion was arrived at that they were nothing more than responsive actions called into play, through the primary or acquired organisation of the nerve centres, by certain forms of peripherical stimulation, independently of any intelligent adaptation of means to ends on the part of the animal itself. From the facts of human physiology and pathology, by which alone the question can be answered, it was concluded that consciousness was inseparable from the activity of the cerebral hemispheres, and that, therefore, however much the responsive actions of the lower ganglia might resemble conscious actions, they did not come within the sphere of truly psychical phenomena.

The destruction of the cerebral hemispheres, by annihilating sensation, ideation, volition, and intelligence in general, reduces the animal to the condition of a complex machine, the activity of which is the immediate or direct result of certain forms of 'ento-' or 'epi-peripherical' stimulation.

But though the functions of the cerebrum have thus been negatively indicated, the whole mechanism of cerebral activity still remains to be investigated. Though it is by means of the cerebrum that we feel and think and will, the question is whether, by physiological or pathological investigation, we can

throw a light on psychological manifestations; whether the cerebrum, as a whole and in each and every part, contains within itself, in some mysterious manner inexplicable by experimental research, the possibilities of every variety of mental activity, or whether certain parts of the brain have determinate functions.

Up to a comparatively recent date, if we except the cumbrous cross-divisions and fanciful localisation of 'faculties' of the phrenological system, the results of experimental physiology and human pathology had been considered as opposed to the localisation of special functions in distinct regions of the cerebral hemispheres.

The experiments of Flourens, the great pioneer in cerebral physiology, led him to the following conclusions with regard to the question of localisation of function :—

'Ainsi 1°, on peut retrancher, soit par devant, soit par derrière, soit par en haut, soit par le côté, une portion assez étendue des lobes cérébraux, sans que leurs fonctions soient perdues. *Une portion assez restrainte de ces lobes suffit donc à l'exercice de leurs fonctions.*

'2°. A mesure que ce retranchement s'opère, toutes les fonctions s'affaiblissent et s'éteignent graduellement; et passé certaines limites, elles sont tout-à-fait éteintes. Les lobes cérébraux concourent donc par tout leur ensemble à l'exercice plein et entier de leurs fonctions.

'3°. Enfin, dès qu'une perception est perdue, toutes le sont; dès qu'une faculté disparaît, toutes disparaissent. Il n'y a donc point de sièges divers ni pour les diverses facultés, ni pour les diverses perceptions. La faculté de percevoir, de juger, de vouloir une chose réside dans le même lieu que celle d'en percevoir, d'en juger, d'en vouloir une autre; et conséquemment cette faculté, essentiellement une, réside essentiellement dans un seule organe.' [1]

The doctrines of Flourens met with very general acceptance as being in accord with at least many well-established facts of clinical medicine, such as the occurrence of extensive disease or injury of brain substance without any appreciable physiological or psychological defect.[2] And there are not wanting

[1] *Système Nerveux*, 1842, p. 99.

[2] On this see the author's *Localisation of Cerebral Disease*, 1878.

some, even at the present day, notably Brown-Séquard,[1] who hold that there is no constant relation between the locality of the lesion and the symptoms which may be manifested :—the same lesion causing most diverse symptoms, and the same symptom occurring in connection with the most diverse lesions.

But to certain careful observers, Bouillaud,[2] Andral,[3] and others, there were many unquestionable facts of clinical medicine, such as limited paralysis in connection with limited cerebral lesions, which appeared wholly inexplicable except on the hypothesis of a differentiation of function in the cerebral hemispheres. And the, in more recent times, established coincidence of aphasia, or loss of speech, with disease of a certain region in the left hemisphere served still further to render the theory of functional equivalence doubtful; though what aphasia really meant in physiological terms, or why in practically symmetrical hemispheres a faculty should be localised in the one, to the exclusion of the other, remained a matter of mystery and dispute.

§ 2. Hughlings Jackson, from a minute and careful study of the phenomena of unilateral and limited epileptiform convulsions, arrived at the conclusion that they were due to irritation, or discharge, of certain convolutions of the opposite cerebral hemisphere functionally related to the corpus striatum and muscular movements. Though he furnished many arguments in favour of his hypothesis, since verified, his views were regarded merely as ingenious speculations, and devoid of any actual proof that the grey matter of the convolutions was really excitable. Experimental physiologists had all failed to obtain evidence of the susceptibility of the cerebral cortex to any of the ordinary stimuli of nerves, mechanical, chemical, thermal, or even electrical. This apparent inexcitability of the cerebral cortex greatly retarded the progress of cerebral physiology. The complementary methods of excitation and destruction, which rendered the study of the functions of the peripheral nervous system a matter of comparative ease, were

[1] 'Comptes Rendus de la Société de Biologie,' 1876 *et seq.*, the *Lancet*, 1876.

[2] *Traité de l'Encéphalite*, p. 279.

[3] *Clinique Médicale*, tome v. p. 569.

not available in the case of the central nervous system, and the determination of the functions of the hemispheres and of their different parts had to be founded only on the results of vaguely established experimental lesions in the lower animals, or on the complex assemblage of phenomena met with in connection with the fortuitous and indefinite experiments of disease in man. Everywhere doubt and discrepancy prevailed. A new era in cerebral physiology was inaugurated by the discovery by Fritsch and Hitzig in 1870 [1] that the application of the galvanic current to the surface of the cerebral hemisphere in dogs gave rise to movements on the opposite side of the body—movements which varied with the position of the electrodes. Subsequently,[2] in the course of experiments undertaken primarily in order to test the views of Hughlings Jackson in reference to the causation of unilateral epileptiform convulsions, I verified and extended the facts first indicated by Fritsch and Hitzig. These have led to much repetition, variation, and controversy, and the results have been that the indications furnished by the electrical irritation of the hemispheres have so guided and directed experimental and clinical research, that the physiology of the brain has made greater advances during the last ten years than in all the previous years of physiology and pathology together.

§ 3. The method principally followed by Fritsch and Hitzig in their researches consisted in applying directly to the surface of the hemispheres, by means of a pair of blunted electrodes, the stimulus of the closing, opening, or commutation of the current of a galvanic pile, of sufficient intensity to cause a distinct sensation when applied to the tip of the tongue. The method employed by myself was the similar application of the electrodes, of the secondary spiral of Du Bois-Reymond's induction coil, connected with a cell of the mean electro-motive power of 1 Daniell. The resistance in the primary coil was such as to give a current of the maximum of 1·9 absolute unit, as estimated for me by my colleague Professor Adams. The induced current generated in the secondary coil at 8 cm.

[1] Reichert u. Du Bois-Reymond's *Archiv*, 1870.

[2] 'Exp. Researches in Cereb. Physiology and Pathology,' *West Riding Lunatic Asylum Reports*, 1873.

distance from the primary spiral was of a strength sufficient to cause a pungent, but quite bearable, sensation when the electrodes were placed on the tip of the tongue. The measurement by the tongue is the most convenient practical test of the intensity of the current, and the best means of regulating the degree of stimulation. In long-continued experiments the failure of battery power may require closer approximation of the secondary to the primary coil, in order to produce the same sensation on the tongue as at first. Owing to my having given the distance of the secondary from the primary alone in the record of my first experiments, without specially calling attention to this circumstance, it has been concluded by Hitzig and others that, in order to produce the effects I have described, I employed currents of enormous intensity, sufficient to cause structural lesions and unlimited conduction to neighbouring and subjacent parts. I have found by repeated experimentation that, with a uniformly acting cell, and the secondary coil at 8 cm., all the effects I have described are easily reproducible. Absolute uniformity, however, cannot be secured, on account of the conditions which modify the excitability of the hemispheres.

That which will cause intense and indefinite action in an animal non-narcotised, will excite only moderate and definite action in an animal sufficiently narcotised to abolish all sense of pain, and no effect at all on an animal deeply anæsthetised. Other conditions also mentioned by Hitzig, *e.g.* the state of the circulation in the brain, greatly modify its excitability, hæmorrhage lowering it in a marked degree. Considerable differences also exist in different animals with respect to the excitability of the hemispheres; and it is only rarely that a complete exploration of the brain can be successfully carried out in any one animal, the excitability of the brain rapidly becoming exhausted during the operations necessary to reach the more concealed and deep-seated regions. The skill with which the operations are made considerably affects the degree of success attainable.

In consequence of these various modifying conditions it is impossible to fix any arbitrary standard, founded on the minimum strength of current necessary to excite any one part in

any given subject of experiment. Various regions of the brain differ in regard to their degree of excitability. A current sufficient to cause decided contraction of the orbicularis oculi will frequently fail to produce any movement of the limbs. By arbitrarily fixing a standard of stimulation which they thought sufficient, Fritsch and Hitzig failed to elicit most important positive results of deep significance in regions of the brain which they choose to call inexcitable. There is no reason to suppose that one part of the brain is excitable and another not. The question is, how the stimulation manifests itself.

Though it is obviously advisable to use no stronger current than is sufficient to produce a definite result, *the measure of the intensity of the stimulus to be employed in each case is the degree of definite and decided localisation of effects uniformly attainable*. It is also necessary to guard against conduction to neighbouring structures, by insulation of the electrodes, and careful removal of the fluid which is apt to collect on the surface.

The mean strength I have found to be given by the fixation of the secondary coil at 8 cm., though frequently less and occasionally some increase is required.

The chief object being to secure efficient stimulation, to call forth in a decided and distinct manner the functional activity of the part to which the electrodes are applied, it would matter little whether we used the galvanic or faradic stimulus, provided they were both equally suitable for this purpose. But this is not the case.

Not only a certain intensity, but a certain duration of the stimulus, is necessary to produce the characteristic effect. The closing or opening shock of the galvanic current, applied to the region of the brain, from which movements of the limbs are capable of being excited, causes only a sudden contraction in certain groups of muscles, but fails to call forth the definite purposive combination of muscular contractions, which is the very essence of the reaction, and key to its interpretation. Fritsch and Hitzig, in their description of the results of their experiments with the galvanic stimulus, did not, in my opinion, sufficiently define the true character of the movements. If the galvanic current is applied for a longer period

than that necessary to cause the momentary closing or opening shock, electrolytic decomposition of the brain substance ensues at the points of contact with the electrodes; an objection from which the faradic stimulus is entirely free. I have in my possession the brains of monkeys and other animals, on which experimentation by the induced current was maintained for many hours, which, with the exception of some degree of hyperæmia consequent on exposure as much as stimulation, are entirely free from structural lesion.

The following experiment will show the comparative efficiency of the galvanic and faradic methods of stimulation:—

Having exposed the brain of a monkey in the region in which I had previously localised the centre of the biceps, excitation of which causes supination and flexion of the forearm, I sought to determine the exact strength of the induced current necessary to produce this definite action, and to compare its effect with that of the galvanic current.

With the single cell already mentioned, and secondary coil at 13 cm., no result followed; secondary at 12 cm., likewise without effect; secondary at 11 cm., slight appearance of outward rotation of the wrist; secondary at 10 cm., faint supination of the hand; secondary at 9 cm., gentle and slow supination and flexion of the forearm; secondary at 8 cm., distinct and decided supination and flexion of the forearm, without any complication with other movements.

The galvanic current was then employed from six cells (small Smee's elements) of Weiss' battery. During closure of the current no result followed, nor when the current was slowly interrupted. With eight cells and slowly repeated interruption spasmodic and sudden jerks of the hand and forearm were observed, but no definite supination or flexion. With ten cells and slowly repeated interruption similar spasmodic movements were caused; but only when the current was rapidly closed and opened did the spasmodic jerks become converted into the continuous action of supination and flexion of the forearm.

To the tongue the sensation communicated by this stimulus was certainly as strong, if not more pungent, than that of the induced current, and at the point of contact of the electrodes

active electrolytic decomposition and evolution of gas began to manifest itself.

This experiment shows that it is not every degree of intensity or every degree of duration of stimulus that is sufficient to excite the due activity of the hemispheres, and that the galvanic method of stimulation is in all respects inferior to that of faradisation. It will be seen also that the intensity of current derived from the secondary coil at 8 cm. is not beyond that requisite for the production of distinct and definite reaction.

§ 4. Though the effects of localised destructive lesions, strictly parallel to those of localised irritation, are of themselves sufficient to dispose of the objections raised, on the score of diffusion of currents, against the view maintained by Hitzig and myself, that the phenomena of electrical irritation are significant of functional excitation of cortical centres as such, yet an examination of the conditions of electrical irritation alone shows how little weight these objections possess.

It has been contended by Dupuy,[1] and others that the movements which are excited by the application of the electrodes to the surface of the hemisphere, are in reality due to conduction of the currents to the real motor centres situated at the base of the brain. He argues that it is impossible to localise the action of the electrical current in the region included within the electrodes, inasmuch as it can be shown that extrapolar conduction extends through the brain substance to a considerable distance. By placing the sciatic nerve of the galvanoscopic frog preparation on the posterior part of the brain, and applying the electrodes to the anterior part of the hemisphere, he found that active contraction of the gastrocnemius muscle resulted, showing that the current had traversed the whole extent of the hemisphere.

The same fact of extrapolar diffusion through the brain substance was also demonstrated, and more accurately by Carville and Duret.[2] By placing non-polarisable electrodes on the hemisphere at a distance from the exciting electrodes, and connecting them with a galvanometer, they found that a

[1] *Examen de Quelques Points de la Physiologie du Cerveau*, 1873.
[2] *Sur les Fonctions des Hémisphères Cérébraux*, 1875.

decided deflection of the needle occurred at the moment of stimulation. Extrapolar conduction through the brain substance is thus proved; but it is no more than what the ordinary laws of conduction through animal tissues would have led one to expect.

This, however, is a very different thing from the conclusion which Dupuy and those who follow him would draw, viz. that it is only to conduction to the basal ganglia that the movements in question are due. Mere vague statements as to the supposed result of irritation of the basal ganglia cannot be allowed to weigh against the actual results of irritation directly applied to them. Irritation of the ventricular aspect of the corpus striatum causes general contraction of the muscles of the opposite side of the body; and it is impossible by applying the electrodes to the surface of this ganglion to produce differentiated contraction in any one muscle or muscular group. Irritation of the optic thalamus produces no movements of any kind, and irritation of the corpora quadrigemina produces dilatation of the pupils and a combination of muscular movements of the head, trunk, and limbs, such as has been already described. We know, therefore, by direct experiment, what irritation of the basal ganglia should produce; but the phenomena of irritation of the cortex are of a very different order. The phenomena of localised and unilateral convulsive movements attributed by Hughlings Jackson to vital irritation of certain regions of the cortex are precisely of the same nature as those induced by electrical irritation of the same regions, and, as has been shown by Franck and Pitres,[1] may be induced by mere mechanical stimulation when the cortex is in a state of inflammatory irritability. It would be absurd to suppose that mechanical irritation under such conditions acts only by conduction to the basal ganglia.

The great and significant feature of the reactions produced by electrical excitation of the cortex is that they are definite and predictable,[2] and vary with the position of the electrodes.

[1] *Progrès Médical*, Jan. 5, 1878.

[2] This is unquestionable, and may be made the subject of lecture demonstration, under the degree of narcotisation necessary to eliminate all spontaneous movements. The experiences of Couty ('Sur le Cerveau Moteur,'

As will be seen in the following chapter, areas in close proximity to each other, separated by only a few millimetres or less, react to the electrical current in a totally different manner. If there were no functional differentiation of the areas under stimulation the diverse effects would be absolutely incomprehensible on any theory of mere physical conduction, which would, under the circumstances, be practically to the same point in all cases. Movements of the limbs can only be excited from certain points, all others being ineffective. No current applied to the prefrontal or occipital regions will cause movements of the limbs, and yet physical conduction to supposed motor centres and tracts at the base is just as easy from these points as from the parietal regions, which react invariably and uniformly. The supposition that it is mere conduction to the corpus striatum and motor tracts which accounts for the movements is further absolutely contradicted by the simple experiment of placing the electrodes on the island of Reil, which immediately overlies the lenticular nucleus. Here we get in nearest proximity to the corpus striatum and internal capsule, and yet no reaction whatever can be induced by currents which are highly effective when applied to the more distant parietal regions.

An interesting observation was made by Carville and Duret during their experiments, which affords another among the numerous proofs that electrisation of the cortex does not act merely by conduction to subjacent ganglia or tracts. In a dog on which they were operating they failed to produce movements by the application of even the strongest currents to regions which in other dogs they had uniformly found readily excitable. The cause of this proved on examination to be the existence of a large cavity, filled with fluid, occupying the medullary substance of the hemisphere between the cortex and the corpus striatum. Physical conduction from the cortex to the corpus striatum was thus in nowise impeded, and the

Archives de Physiologie, Oct. 1883) to the contrary are doubtless due to his radically vicious method of operating without anæsthetics: 'Les animaux dont je me suis servi ont été presque toujours laissés normaux, sans anæsthésie, sans immobilisation' (p. 267). Results obtained under such conditions do not require further consideration.

connections between the corpus striatum and cerebral peduncle were intact; yet, owing to the destruction of the medullary fibres, the cortical centres could not transmit any impulse downwards, however strongly excited. It is impossible, therefore, to explain away the results of electrical irritation of the cortex by mere conduction to subjacent ganglia or motor tracts, even though a certain amount of extrapolar diffusion is demonstrable. But mere physical diffusion is not equivalent to diffuse stimulation. I have shown that it is not any or every degree of stimulation which is sufficient to excite the activity of the cortex. A strength of current capable of inducing the most violent tetanic spasm if applied to a motor nerve has no appreciable action on the cerebral centres. Hence, though physical conduction may occur in the brain substance, effective stimulation will only occur at the point where the current reaches the necessary intensity, and that is in the intrapolar region. Risks of diffusion, however, must always be borne in mind as a possible source of error, but they can be eliminated by frequent repetition of the experiments, working with the minimum effective current and similar obvious precautions, which all competent investigators naturally take.

§ 5. It would be a matter of indifference, as regards the great question of differentiation of function in the cerebral cortex, if it should appear that it is not the grey matter of the cortical regions which is really excitable, but the cone of subjacent medullary fibres distributed to them. For, if the medullary fibres are differentiated in function, the regions to which they are distributed must be similarly differentiated, unless we are to suppose that the grey matter is merely so much inert stuff; a supposition which, however absurd, is, nevertheless, the logical outcome of the views propounded by some writers on this question. That the medullary fibres are excitable has been proved, but the excitability of the corresponding cortical regions is not thereby excluded; and as a matter of fact, as will be seen, is capable of satisfactory demonstration.

It was first shown by Burdon Sanderson[1] that, after removal of the cortex, electrical stimulation of the medullary

[1] *Proceed. Royal Soc.*, June 1874.

fibres thus laid bare caused movements like those resulting from the application of the electrodes to the respective regions of the cortex themselves. This has been confirmed by the experiments of Braun,[1] Putnam,[2] Carville and Duret,[3] Albertoni and Michieli,[4] Franck and Pitres,[5] Richet,[6] and others; so that we may regard it as satisfactorily established that the medullary fibres are functionally differentiated paths of communication between the cortex and the periphery. They stand to the cortical matter precisely in the same relation as the anterior spinal roots do to the anterior horns of the spinal cord. When the anterior horns are diseased (as in anterior polio-myelitis), or the anterior roots divided, the motor nerves in the course of four to five days entirely lose their excitability and undergo complete degeneration. This important fact was first demonstrated by Albertoni and Michieli, who found that after removal of the grey matter of the cortex the medullary fibres, at first excitable, ceased after an interval of from four to five days to respond to the strongest electrical currents. And it has now been established that after purely cortical lesions [7] degeneration occurs in the corona radiata and pyramidal tracts down the whole extent of their course in the spinal cord. Though the direct excitability of the anterior horns may be questionable, no one doubts the excitability of the anterior roots. But no one doubts the motor functions of the anterior horns on that account. Yet among other ridiculous objections to the motor functions assigned to certain cortical regions it has been argued that they ought to conform to the same laws as regulate the excitability of motor nerves. The excitability of nerve centres and nerve tracts is not only not necessarily the same, but, in reality, it is the very point of

[1] *Centralblatt f. d. med. Wissensch.*, 1874.

[2] *Boston Med. and Surg. Journal*, 1874.

[3] 'Sur les Fonctions des Hémisphères Cérébraux,' *Archives de Physiologie*, 1875.

[4] 'Sui Centri Cerebrali di Movimento,' *Lo Sperimentale*, 1876.

[5] *Soc. de Biologie*, 1877.

[6] *Sur les Circonvolutions Cérébrales*, 1878.

[7] See the facts and experiments by the author and Professor G. Yeo, *Trans. Intern. Med. Congress*, 1881, vol. i.; *Discussion on Localisation*, p. 231; and 'On the Effects of Lesions of Different Regions of the Cerebral Hemispheres,' *Philosoph. Trans.*, Part II. 1884.

difference by which the direct excitability of the cortical grey matter can be established.

Putnam found that a stronger current was necessary to excite the medullary fibres than the corresponding cortical centre. On replacing the removed cortical lamina, and applying the formerly effective current, no action whatever resulted. It is possible, however, as Carville and Duret have contended, that the necessity of intensifying the current when the cortex has been removed is due to the hæmorrhage that occurs, and the consequent tendency to diffusion when the electrodes are placed on the oozing surface.

Franck and Pitres likewise find in non-narcotised animals that the excitability of the cortical centres is greater than that of the corresponding medullary fibres; but Richet states that in narcotised animals the medullary fibres are more excitable than the cortical centres. The experiments of Bubnoff and Heidenhain [1] confirm those of Richet, and show that during the narcosis produced by morphia the medullary fibres are more readily excitable than the corresponding cortical centres. It is possible that this may be the explanation of the fact, signalised by Hitzig, that the anodal closure was more effective than the cathodal closure in his experiments with the galvanic current. The stimulus in this case would proceed from the virtual cathode established in the deeper and more excitable subcortical regions (see p. 197). Deep narcosis, however, abolishes the excitability both of the grey matter and the subjacent medullary fibres, so that no reaction whatever occurs on the application of currents otherwise effective. It has, however, been asserted by Marcacci [2]—whose experiences in this and many other respects appear altogether unique—that, even after freezing the cortex, electrical stimulation is still effective, and causes the same movements as before. This assertion has been completely refuted by Varigny,[3] who found after refrigeration of a given region that no ordinary stimulation was capable of exciting the movements formerly readily excitable; and that, when the current was intensified

[1] Pflüger's *Archiv f. Physiologie*, 1881.
[2] *Archives Italiennes de Biologie*, tome i., 1882.
[3] *L'Excitabilité Electrique des Circonvolutions Cérébrales*, 1884.

beyond all limits of localised irritation, general agitation was produced everywhere *except* in the parts governed, and ordinarily alone thrown into action, by stimulation of the region in question.

Besides the differences which appear to exist in respect to the relative excitability of the grey matter and medullary fibres, there are others of greater importance which clearly establish and differentiate the independent excitability of the cortex from that of the medullary fibres. It was first shown by Franck and Pitres that between the moment of excitation and the resulting movement there elapses an interval, capable of exact measurement. This interval, after deducting the time necessary for the transmission of the impulse through the spinal cord and motor nerves, indicates a retardation in the cortex of 0·045 second. When the grey matter is removed, and the stimulus is applied to the medullary fibres, the period of retardation diminishes to 0·03 second, or about one-third less. They have further shown—and their observations have been confirmed by Richet, Bubnoff and Heidenhain, Varigny, &c.—that the grey matter of the cortex, like nerve centres in general, is capable of storing up, and responding to a succession of stimuli individually insufficient to excite action. Irritation of the cortex frequently responds in a succession of discharges of an epileptiform nature—a phenomenon which never occurs when the medullary fibres alone are stimulated. The duration of the effect in the latter case is strictly proportional to the duration of the electrical excitation. Bubnoff and Heidenhain have further demonstrated a characteristic difference between the muscular curves registered by stimulation of the cortex and medullary fibres respectively. In the latter case the curve rises abruptly, and is of short duration; while in the former it rises more gradually, and is much more prolonged. These differences conclusively prove the independent excitability of the cortex as such. But, as before remarked, it was not necessary to prove this, *qua* the question of differentiation of function in the cortex. For the admitted differentiation of the medullary fibres, and the dependence of their functional vitality on the integrity of the corresponding cortical centres, necessarily implies a corresponding differen-

tiation in the regions to which they are distributed. In addition to the various facts above mentioned, which show that the cortex as such is excitable, and that it is not merely on physical conduction to the excitable medullary fibres that the movements depend, we may adduce the interesting experiments of Soltmann[1] on new-born dogs. In these it is not possible to excite movements of the limbs from the cortex before the tenth day, at which time the foreleg is generally capable of being stimulated to action. Yet several days before this, it is easy, by comparatively weak currents, to excite the same movement by irritation directly applied to the subjacent medullary fibres. That the cortex is not merely a physical conductor of the electrical current to the excitable medullary fibres is thus clearly apparent.

With these considerations on the methods of investigation I propose in the next chapter to describe the phenomena observed on electrical irritation of the cerebral hemispheres in different orders of animals, and in the next place to endeavour to interpret them in the light of the complementary method of destruction. The details of individual experiments are spared, except on points of uncertainty or dispute. For fuller data on which the statements and views maintained by the author are based reference is made to the undermentioned papers and memoirs.[2]

[1] *Jahrbuch für Kinderheilkunde*, 1876. On this see further Chap. VIII. § 3.

[2] (1) 'Experimental Researches in Cerebral Physiology and Pathology,' *West Riding Lunatic Asylum Reports*, vol. iii. 1873.

(2) 'Experiments on the Brain of Monkeys,' First Series, *Proceedings of the Royal Society*, No. 161, 1875; *ibid.* Second Series, *Philosoph. Transactions*, vol. ii. 1875; 'On the Effects of Lesions of Different Regions of the Cerebral Hemispheres' (in conjunction with Professor G. Yeo), *Philosoph. Transactions*, Part II. 1884.

CHAPTER VIII.

PHENOMENA OF ELECTRICAL IRRITATION OF THE CEREBRAL HEMISPHERES.

PART I.—*Experiments on Monkeys.*

§ 1. THE surface of the cerebral hemispheres in macaques, the species of monkeys usually employed in these experiments, is divided into certain lobes and convolutions by certain primary and secondary fissures or sulci (figs. 67, 68). Different systems of nomenclature have been adopted by different writers, and different views have been expressed in reference to the homologies of the various sulci and convolutions. As it is not necessary for mere topographical description to enter into questions of homology, I have in the following references mainly followed the nomenclature of Gratiolet, with the addition of such synonyms as are in most common use among writers on cerebral topography.

Of the primary fissures there are three readily distinguishable on the convex aspect, the *fissure of Sylvius* (fig. 67, A), the *fissure of Rolando*, or *central fissure* (fig. 67, B), and the *parieto-occipital* or *perpendicular fissure* (fig. 67, C), also called the *simian fissure*.

The *frontal lobe* (fig. 67, F L) includes all in front of the fissure of Rolando, or central fissure.

This is divided by secondary fissures, one of which anterior to and almost parallel with the fissure of Rolando is termed the *antero-parietal* (Huxley) or *præcentral sulcus* (Ecker) (fig. 67, *a p*), and two others running almost at right angles to this. The upper one (fig. 67, *s f*), which is a mere prolongation forwards of the præcentral sulcus, is the *supero-frontal sulcus*; the lower (fig. 67, *i f*) is the *infero-frontal sulcus*.

The convolution included between the central and præ-central sulci is termed the *ascending frontal*, or *præcentral convolution* (fig. 67, AF). At the upper extremity of this convolution there is generally a well-defined nail-shaped depression or rudimentary sulcus. By the supero-frontal and infero-frontal sulci the convex aspect of the rest of the frontal lobe is divided into three convolutions, termed by Gratiolet

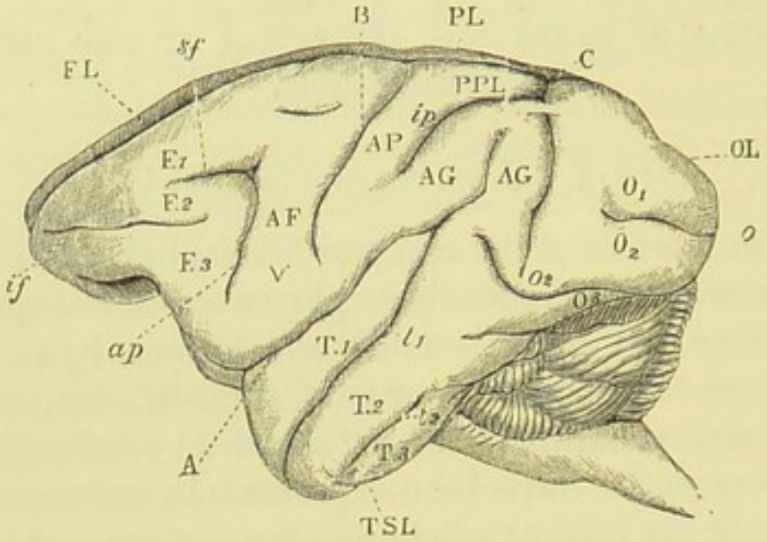


FIG. 67.—Left Hemisphere of the Brain of the Monkey (Macaque).—A, the fissure of Sylvius. B, the fissure of Rolando. C, the parieto-occipital fissure. FL, the frontal lobe. PL, the parietal lobe. OL, the occipital lobe. TSL, the temporo-sphenoidal lobe. F_1, the superior frontal convolution. F_2, the middle frontal convolution F_3, the inferior frontal convolution. *sf*, the supero-frontal sulcus. *if*, the infero-frontal sulcus. *ap*, the antero-parietal sulcus. AF, the ascending frontal convolution. AP, the ascending parietal convolution. PPL, the postero-parietal lobule. AG, the angular gyrus. *ip*, the intra-parietal sulcus. T_1, T_2, T_3, the superior, middle, and inferior temporo-sphenoidal convolutions. t_1, t_2, the superior and inferior temporo-sphenoidal sulci. O_1, O_2, and O_3, the superior, middle, and inferior occipital convolutions. O_1, O_2, the first and second occipital fissures.

the *superior*, *middle*, and *inferior frontal* convulutions respectively [1] (fig. 67, F_1, F_2, F_3).

[1] Though the division of the frontal lobe in the monkey into three convolutions is perfectly distinct, and though there is thus an apparently complete homology between the frontal convolutions of the human and simian brain, reasons have been advanced by Bischoff against this being regarded as a true homology. He would make what is here termed the infero-frontal sulcus the homologue of the human supero-frontal sulcus, and thus divide the frontal lobe into only two convolutions, corresponding with the superior and middle frontal convolutions in man. The inferior or third frontal convolution would thus be considered as entirely absent in the ordinary simian brain. In the brain of the gorilla, however, a rudimentary third frontal convolution is capable of being traced (see Chap. XIII.) The terms used in the text may, however, be employed without prejudice to the questions of homology.

The inferior or orbital aspect of the frontal lobe sometimes receives the special designation of the *orbital lobule* (fig. 68, F O).

The *parietal lobe* (fig. 67, P L) is bounded by the fissure of Rolando anteriorly, and by the parieto-occipital fissure posteriorly. It is divided by the *intraparietal sulcus* (fig. 67, *i p*) into three divisions or convolutions: viz. the *ascending parietal* or *postcentral* convolution (fig. 67, A P), bounded by the fissure of Rolando in front and by the vertical portion of the intraparietal sulcus behind; the *postero-parietal* or *superior parietal lobule* (fig. 67, P P L), which is essentially the expanded base of the ascending parietal convolution; and the *inferior parietal lobule* or *angular gyrus* (fig. 67, A G), which forms an arch over the usually conjoint extremities of the Sylvian (A) and first temporo-sphenoidal fissures (t_1).

The lower extremity of the anterior limb of the angular gyrus sometimes receives the name of the *supramarginal gyrus*, but it is not in the brain of the macaque sufficiently differentiated to require a special designation.

The *temporo-sphenoidal* or *temporal lobe* (fig. 67, T S L) lies behind and below the fissure of Sylvius. It is divided by two sulci, the *superior* (t_1) and *inferior* (t_2) *temporal sulci*, into three convolutions—the *superior*, *middle*, and *inferior temporo-sphenoidal* convolutions (T_1, T_2, T_3).

The *occipital lobe* (fig. 67, O L) lies behind the parieto-occipital fissure, and is more or less continuous, by certain annectent or bridging convolutions, with the parietal and temporo-sphenoidal lobes. Two fissures running horizontally, more or less parallel to each other, viz. the *first* and *second occipital fissures* (fig. 67, o_1 and o_2), divide the occipital lobe into three convolutions; viz. the *superior*, *middle*, and *inferior occipital convolutions* (o_1, o_2, o_3).

The middle occipital convolution is continuous in front with the posterior limb of the angular gyrus by a well-defined annectent gyrus; and the inferior occipital convolution is continuous with the middle temporal convolution, the annectent gyrus being frequently distinctly marked by a shallow sulcus below and parallel to the second occipital fissure.

When the lips of the fissure of Sylvius are separated, another lobe is displayed, called the *central* or *insular lobe*, or

island of Reil (fig. 25, *i* R). This lobe is moulded on, and conceals the lenticular nucleus, or extra-ventricular nucleus of the corpus striatum. In the monkey the surface of this lobe is smooth, and not, as in man, marked by convolutions (*gyri breves*).

On the internal or mesial aspect of the hemisphere certain important fissures and convolutions are differentiated. The convolution which runs concentric, and in immediate relation, with the corpus callosum (fig. 68, c c) is termed the *gyrus fornicatus* (fig. 68, GF). It commences on the mesial aspect of the frontal lobe at the anterior perforated space, embraces the

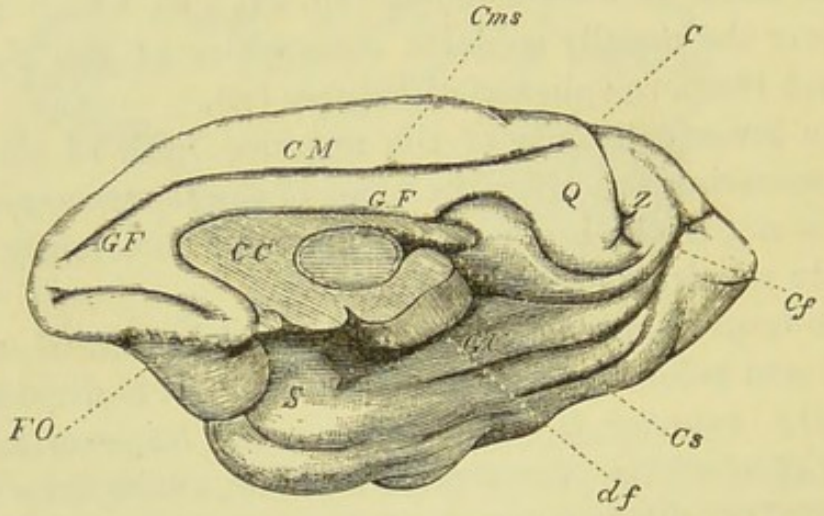


FIG. 68.—The Internal Aspect of the Right Hemisphere of the Monkey (Macaque).—CC, the corpus callosum divided. C, the internal parieto-occipital fissure. *Cms*, the calloso-marginal fissure. *Cf*, the calcarine fissure. *df*, the dentate fissure. *Cs*, the collateral fissure. GF, the gyrus fornicatus. CM, the marginal convolution. GU, the uncinate convolution. S, the crochet, or subiculum cornu Ammonis. Q, the quadrilateral lobule, or præcuneus. Z, the cuneus. FO, the orbital lobule.

corpus callosum, and interrupted superficially by the calcarine fissure[1] (*Cf*) becomes continuous with the *gyrus hippocampi* or *uncinate gyrus* (Huxley) (fig. 68, G U). The anterior extremity of this gyrus is recurved at the point, where it joins with the fimbria of the fornix and fascia dentata, and forms a crochet or hook, and hence has received the name of the *uncus*—also by some called the gyrus uncinatus. The whole of this region, variously subdivided by different authors, constitutes Broca's *falciform lobe* (*grand lobe limbique*) (fig. 68, G F, G U, S).

[1] In man the calcarine fissure does not run into the dentate fissure, but leaves a small portion which is termed the *isthmus gyri fornicati*. In all the brains of the macaque which I have examined the fissures are, however, continuous with each other.

The falciform lobe is bounded above by the *calloso-marginal sulcus* (fig. 68, *C m s*). Between this and the margin of the hemisphere is a convolution which forms the mesial aspect of the frontal and parietal lobes, and is termed the *marginal convolution* (fig. 68, c m). The posterior extremity of the calloso-marginal sulcus turns upwards towards the margin of the hemisphere, somewhat behind the upper extremity of the fissure of Rolando (indicated in fig. 68 by a slight notch). Between the posterior extremity of the calloso-marginal sulcus and the internal *parieto-occipital fissure* (fig. 67, c) an irregularly shaped lobule is termed the *quadrilateral lobule*, or *præcuneus*, and behind it, and bounded beneath by the calcarine fissure (fig. 68, *C f*), is the *cuneus* (fig. 68, z).

The *calcarine fissure* (fig. 68, *C f*) marks the position of the *calcar avis*, or hippocampus minor, in the posterior cornu of the lateral ventricle. It is continuous in front with the *dentate* or *hippocampal fissure* (fig. 68, *d f*), which marks the position of the fascia dentata and hippocampus major in the descending cornu of the lateral ventricle. The gyrus hippocampi is bounded by this fissure above, and separated from the inferior temporo-sphenoidal convolution by the *occipito-temporal* or *collateral sulcus* (fig. 68, *C s*).

§ 2. The points of electrical irritation are indicated on the accompanying figures (figs. 69–71) by areas or circles which mark the extent of the regions stimulation of which gives rise to certain more or less definite and constant movements. The areas have no exact line of demarcation from each other, and where they adjoin stimulation is apt to produce the conjoint effect peculiar to each. This occurs all the more readily the greater the intensity of the current, and also when the irritability of the brain has become heightened and a tendency to epileptiform explosions has been induced. Variations also occur in respect of the completeness of the reaction. A slight stimulus of short duration causes only a part of a complex action, which is manifested in its completeness when the stimulus is of somewhat greater intensity and duration. The point of limited action is most correctly indicated by the centre of the circle or area. The boundaries were determined by frequently repeated application of the electrodes on and around

these areas. For the facts of individual experiments the reader is referred to the author's above-cited memoir, 'Experiments on the Brain of Monkeys' (*Proceedings Royal Society*, No. 161, 1875).

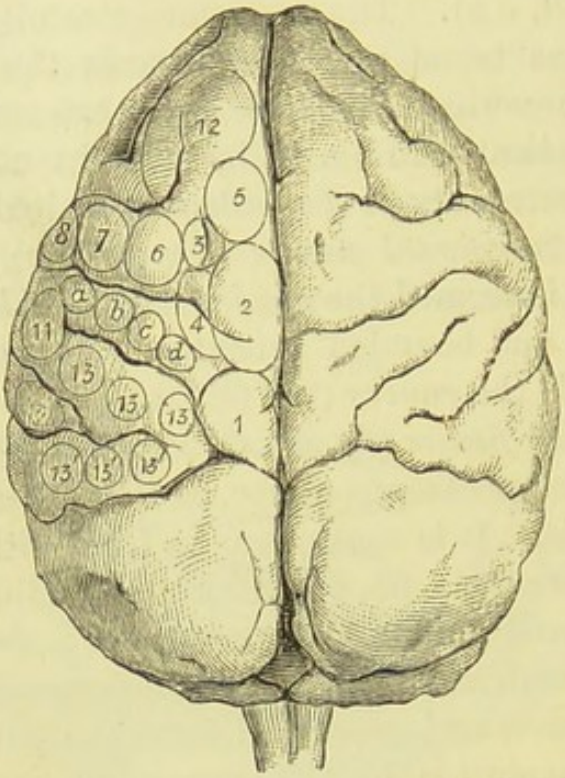


FIG. 69.—Upper Surface of the Hemispheres of the Monkey. (Royal Soc.)
The circles and included numerals are explained in the text.

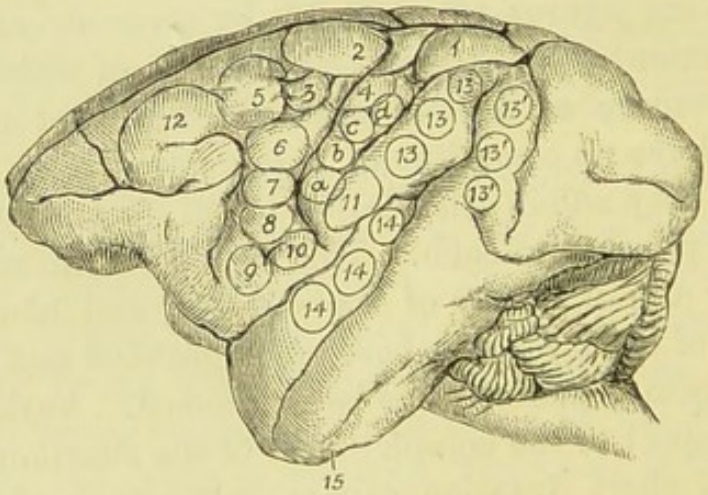


FIG. 70.—The Left Hemisphere of the Monkey. (Royal Soc.)
The circles and numerals have the same signification as in last figure.

The following are the phenomena most constantly observed:—

(1). On the superior or postero-parietal lobule.

The opposite hind limb is advanced as in walking—the thigh being flexed on the pelvis, the leg extended, with dorsal flexion of the foot, and spreading, or extension, of the toes. Occasionally the action is limited to the foot, this being dorsally flexed and the toes expanded.

(2). On the upper extremity of the ascending parietal, and adjoining portion of the ascending frontal convolution.

Flexion with outward rotation of the thigh, rotation inwards of the leg, with flexion of the toes—the action being such as is seen when a monkey makes a grasping movement, or scratches its chest or abdomen with its foot. Various degrees of this action may be seen according to the strength and duration of the stimulus; but the above is the complete action uncomplicated by other movements, except certain synergic movements of the trunk necessary to the full execution of the action in question. The action is similar to that caused by stimulation of the sixth lumbar root of the crural plexus (fifth in man).

(3). Close to the semilunar sulcus at the upper extremity of the ascending frontal convolution.

Here movements similar to those under (1) and (2) are produced, and in some cases also *the tail is moved*. I have not been able to dissociate the movements of the tail from those of the trunk and hind limb.

(4). Behind (3) and below (2) on the adjacent margins of the ascending frontal and ascending parietal convolutions at their upper portion.

The opposite arm is adducted, extended, and retracted, the hand pronated. By this action the hand is struck backwards, almost exactly in the same way as occurs on stimulation of the seventh cervical root of the brachial plexus. It is an action which if the hand were the fixed point would by the action of the latissimus dorsi raise the body upwards and forwards, as in climbing a trapeze.

(5). On the ascending frontal convolution at the base of the superior frontal.

Extension forwards of the opposite arm, as if the animal tried to reach or touch something in front.

Areas (*a*) (*b*) (*c*) (*d*) various points on the ascending parietal convolution.

Clenching of the fist.—With slight stimulation the action begins in the thumb and index finger, followed on longer stimulation by flexion of all the fingers and firm clenching of the fist. With the closure of the fist is associated the synergic action of the extensors of the wrist and fingers, but centres for the individual flexors and extensors could not be differentiated.

(6). On the ascending frontal convolution at the bend or knee of the præcentral sulcus.

Flexion and supination of the forearm—the completed action bringing the hand up to the mouth. The movement is essentially the same as that which occurs on stimulation of the sixth cervical root of the brachial plexus.

The action is apt to be associated with (7) and occasionally, when the irritation is near the fissure of Rolando, with clenching of the fist.

(7). On the ascending frontal convolution below (6).

Retraction and elevation of the angle of the mouth—the action of the zygomatic muscles.

(8). On the ascending frontal convolution below (7).

Elevation of the ala of the nose and upper lip—associated with depression of the lower lip, so as fully to expose the canine teeth.

(9) and (10). On the lower extremity of the ascending frontal convolution.

Opening of the mouth, with protrusion (9) *and retraction* (10) *of the tongue.*—These movements are occasionally repeated for some time after the electrodes are withdrawn. The movements are bilateral.

(11). On the lower extremity of the ascending parietal convolution.

Retraction of the angle of the mouth.—The action is that of the platysma myoides, and when this is strong the head is drawn slightly to the side.

(12). Including the posterior half or two-thirds of the superior and middle frontal convolutions.

The eyes open widely, the pupils dilate, and head and eyes

turn to the opposite side.—Occasionally this action is apt to be associated with that described under (5).

Prefrontal region.

As a rule, stimulation of the frontal lobes in advance of (12) as well as of the orbital lobule was without obvious effect.

In one case, however, I had observed a movement of the eyes to the opposite side on irritation of the prefrontal region, and in two others, which I have recently experimented on, the same results were obtained, viz. movement of the eyeballs to the opposite side. I am therefore disposed to consider these movements as in direct causal relationship with irritation of the prefrontal regions, and not accidental or mere coincidences.

(13) and (13′) on the anterior and posterior limb of the angular gyrus respectively.

The eyes move to the opposite side, with an upward or downward deviation, according as the electrodes are on (13) or (13′) respectively. Usually also the pupils become contracted, and there is occasionally a tendency to closure of the eyelids, if the eyes are already open at the time of stimulation, as if under the stimulus of a strong light. Luciani and Tamburini[1] have occasionally seen the pupils dilate instead of contract, but differences of this kind are unimportant, as the pupils will vary according to the condition of the animal at the time. It is well known that during sleep the pupils are contracted, but dilate on the individual being suddenly awakened, and then again contract under the influence of the light which falls on them. In like manner the sudden stimulation of the angular gyrus may in a monkey at the time fully awake cause contraction of the pupil; while in another asleep, or nearly so, the first effect will be dilatation from roused attention.

Sometimes the head turns with the eyes to the opposite side.

(14). On the superior temporo-sphenoidal convolution.

Pricking of the opposite ear, head and eyes turn to the opposite side, pupils dilate widely.

[1] *Sui Centri Psico-motori Corticali* (1878), and *Sui Centri Psico-sensori Corticali* (1879).

(15). On the anterior and inner aspect of the uncinate gyrus (subiculum cornu Ammonis).

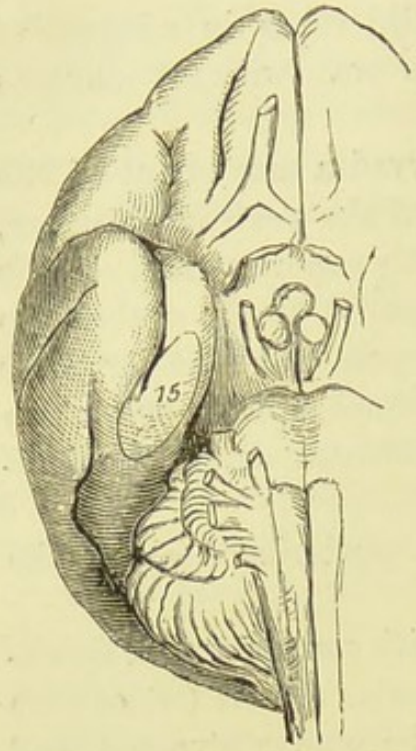


FIG. 71.—Base of the Brain (right side) of the Monkey. (Roy. Soc.)

Torsion of the lip and semiclosure of the nostril on the same side, as when the interior of the nostril is irritated by some pungent odour.

Irritation of the middle temporo-sphenoidal convolution I have found in general to be without any obvious reaction, except towards the lower extremity, where in several instances movements of the tongue, cheek pouches, and jaws were induced very like those which are characteristic of tasting.

Island of Reil or Central Lobe.

Stimulation causes no motor reactions.

When the irritation is increased, and the margins of the fissure of Sylvius are irritated, some movements of the mouth and tongue occur—explicable by the proximity of areas (9) and (10).

Occipital Lobe.

I have never obtained any reactions on stimulation of the occipital lobes, while at the same time, and with the same strength of current, the reactions above described were one or all readily obtained. In one case the insinuation of the electrodes underneath the inferior occipital convolution, approximately on the upper part of the gyrus hippocampi, caused uneasy-like movements of the hind legs and tail, while the animal looked towards its opposite hind leg, and occasionally uttered a plaintive cry, as if in pain or annoyance. What was exactly irritated in this case could not be ascertained, owing to the difficulty of exposure of the parts.

Marginal Convolution.

In the only case in which I specially investigated this convolution I found that irritation of its fronto-parietal portion gave rise to movements of the head and limbs similar to those

obtained by stimulation of the corresponding regions on the convex or external aspect.

Important contributions to the physiology of this region have been recently made by Horsley and Schäfer.[1] They have found that the marginal convolution is excitable except in the prefrontal region—anterior to (12) above described. When the anterior portion (fig. 72, A) of the excitable region was stimulated, the resulting movements affected the upper limb, and in one or two instances the muscles of the head and neck; when the middle (fig. 72, B) of the excitable region was stimulated, the muscles chiefly or primarily affected were

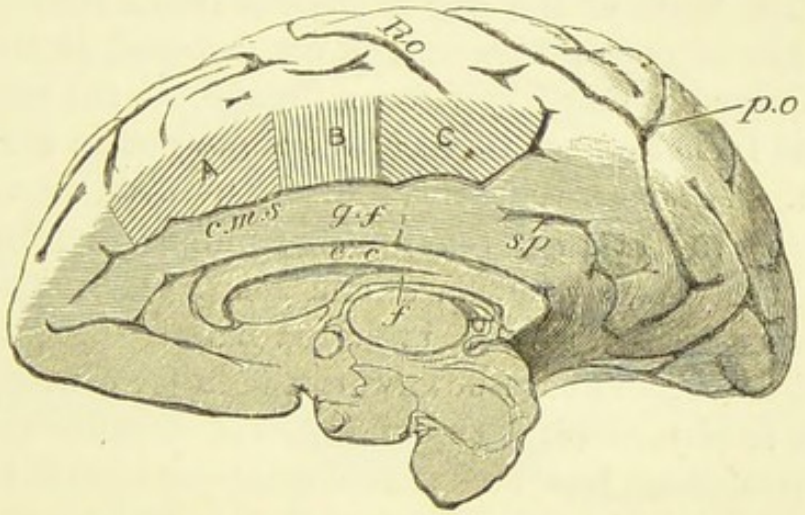


FIG. 72.—Mesial Aspect of the Right Hemisphere of the Monkey, showing the Motor Areas of the Marginal Convolution, according to Horsley and Schäfer.—A, B, C, motor areas of the marginal convolution. *cc*, corpus callosum. *cms*, calloso-marginal fissure. *gf* gyrus fornicatus. *po*, parieto-occipital fissure. *Ro*, fissure of Rolando. *sp*, subparietal sulcus.

those of the trunk (erector spinæ, abdominal muscles, &c.) whilst when the posterior region (fig. 72, C) was stimulated, the muscles of the lower limb alone were called into action. They arrange the movements from before backwards in the following order: viz. (1) movements of the forearm; (2) movements of the humerus and scapula; (3) movements, chiefly rotation and flexion, of the upper part of the trunk; (4) movements of the lower part of the trunk and abdomen; (5) movements of the pelvis; (6) movements of the hip;

[1] 'On the Functions of the Marginal Convolution' (Preliminary Communication), *Proceedings of the Royal Society*, No. 231, March 1884.

(7) movements at the knee; (8) movements at the ankle joint; (9) movements of the toes.

Gyrus Fornicatus.

No movements resulted from stimulation of this convolution by means of electrodes insulated so as to avoid irritation of other regions.

Corpus Callosum.

Stimulation of this also is entirely negative as regards outward manifestations.

Part II.—*Experiments on Dogs.*

§ 3. The brain of the dog is divided on its convex aspect into a series of convolutions which are disposed, in the main, archwise over the *fissure of Sylvius* (fig. 73, A), the position of which and homology with that of the simian brain are readily apparent. These convolutions, four in number, were termed by Leuret[1] the *external convolutions*, numbered from below upwards, the *first*, *second*, *third*, and *fourth* external convolutions respectively. I have preferred naming them in the reverse order, from above downwards, both for convenience in reference to physiological experiment, and because the three upper convolutions have their homologues—at least in a physiological sense—on the convex aspect of the simian and human brain, whereas the lowermost has not. In addition the differentiation into four external convolutions is not always clear in some of the carnivora, owing to the fusion of the two lowermost, so that to commence the enumeration from below is obviously inconvenient.

The various fissures, sulci, convolutions, and their parts have been named with great elaborateness and detail by different writers;[2] but for purposes of description I retain the nomenclature of Leuret, giving such synonyms as seem to me of more especial importance or significance.

The *first external convolution* (fig. 73, 1) in the frontal region

[1] Leuret and Gratiolet, *Anat. Comp. du Système Nerveux*, 1839–1857.

[2] See on this subject a paper by Langley, 'The Structure of the Dog's Brain,' *Journal of Physiology*, vol. iv., in which the various systems of nomenclature are collated.

makes a bend round a fissure which is generally well-marked in the brains of the carnivora, viz. the *crucial sulcus* (Leuret), or *frontal sulcus* (Owen) (fig. 73, B).

This constitutes what I have termed the *sigmoid gyrus*, a term first employed by Flower in his description of the brain of the Proteles.[1] In the cat (fig. 77) the sigmoid gyrus is composed of a simple anterior and posterior limb. In the dog each limb is again subdivided by a slight *precrucial*, and *postcrucial* sulcus. The first external convolution forms the upper margin of the hemisphere and descends on the mesial aspect to a sulcus (the *sub-parietal sulcus*), which divides it from the falciform lobe, and of which the crucial sulcus is the

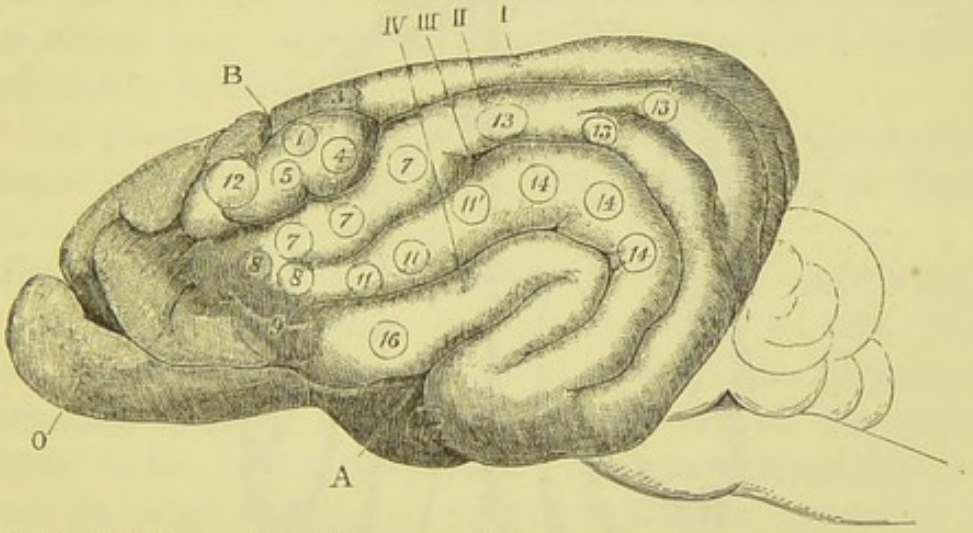


FIG. 73.—Left Hemisphere of the Brain of Dog.—A, the fissure of Sylvius. B, the crucial sulcus. O, the olfactory bulb. I. II, III, IV, indicate the first, second, third, and fourth external convolutions respectively. The circles and numerals are explained in the text. (1), (4), and (5) are on the *sigmoid gyrus*.

anterior extremity continued on the convex aspect of the hemisphere.

The *second external convolution* (fig. 73, II), separated from the first by the superoir curved fissure, runs parallel with it, and posteriorly is divided into two limbs by a secondary fissure. The frontal extremity of the superior curved fissure is sometimes termed the *coronal fissure* (fig. 73, above (7)), and the corresponding frontal portion of the second external convolution is similarly termed the *coronal gyrus* (fig. 73, (7)).

The *third external convolution* (fig. 73, III) is also termed the *supra-Sylvian convolution*; while the *fourth external convolu-*

[1] *Proceed. Zoolog. Soc.*, Nov. 1869.

tion (IV) which immediately arches over the fissure of Sylvius commonly receives the name of the *Sylvian convolution*.

The convolutions fuse with each other more or less posteriorly as well as anteriorly. The anterior extremities of the three lowermost convolutions end in a gyrus (the *anterior composite* (Langley), ascending obliquely (fig. 73, (9)). The anterior boundary of this is formed by a fissure which is termed the *præ-Sylvian* or *supra-orbital fissure*.

The excitation of definite movements by electric irritation of the cortex was first demonstrated on the brain of dogs by the important researches of Fritsch and Hitzig in 1870.[1]

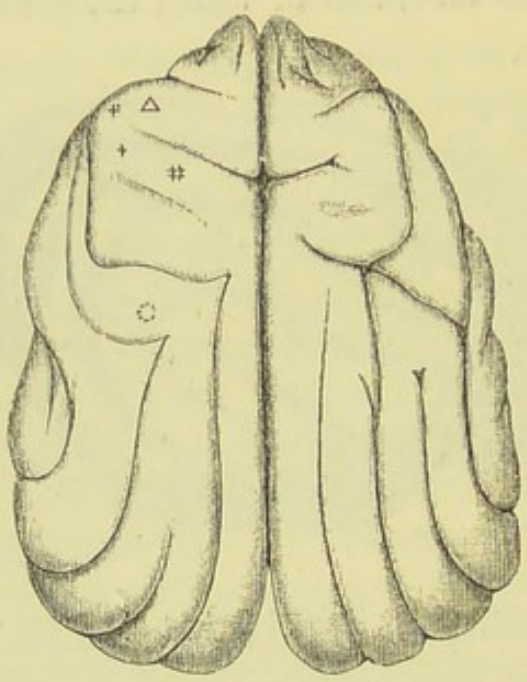


FIG. 74.—Figure of the Brain of the Dog, illustrating Fritsch and Hitzig's researches.

The following extract and accompanying figure (fig. 74) are from the original description of the results arrived at by Fritsch and Hitzig, prior to the localisation experiments on various animals described in this chapter.

'The centre for the neck-muscles (fig. 74, △) lies in the lateral part of the prefrontal gyrus, at the point where the surface of this convolution abruptly descends. The outermost extremity of the postfrontal gyrus contains, in the neighbourhood of the lateral end of the frontal fissure (fig. 74, +), the centre for the extensors and adductors of the fore limb.

[1] Reichert u. Du Bois-Reymond's *Archiv*, 1870, Heft 3.

Somewhat behind the same, and nearer the coronal fissure (fig. 74, +), lie the ruling centres for the flexion and rotation of the limb. The centre for the hind leg (fig. 74, ‡‡) is also found in the postfrontal gyrus, but nearer the middle line than that of the fore leg, and somewhat further back. The facial (fig. 74, ☼) is innervated from the middle part of the super-Sylvian gyrus. This region generally has an extension of over 0·5 centimetre, and stretches before and behind the bend over the Sylvian fissure. We must add that we did not always succeed in setting the neck-muscles in action from the first-mentioned point. The muscles of the back, tail, and abdomen we have often enough excited to contraction from points lying between those marked, but no circumscribed point from which they could be individually stimulated could be satisfactorily determined.

'The whole of the convexity lying behind the facial centre we found absolutely unexcitable, even with altogether disproportionate intensity of current.'

Hitzig, in subsequent experiments,[1] while confirming in many respects the results described by me in the 'West Riding Asylum Reports,' vol. iii., questions the accuracy of others, especially as regards the excitability of the regions posterior to the fissure of Sylvius. The phenomena described by me he attributes to vague conduction of currents. In support of his view he endeavours to show that the phenomena are discordant with each other, and that my experiments would localise different motor centres in essentially the same regions, and motor centres for the same movements in widely different parts of the brain. These discrepancies which Hitzig discovers do not exist in reality, but only in his own method of reading the facts. The mere fact that movements result from stimulation of a given part of the hemisphere does not necessarily imply that the same is a motor centre in the proper sense of the term. It will afterwards be shown that the movements which result from stimulation of the regions in question are expressive of sensation, and that the character of the movements furnishes an important index to the nature of the sensation.

[1] *Untersuchungen ü. das Gehirn*, Berlin, 1874.

The movements, therefore, being of the character of associated or reflex indications of sensation, will vary in extent according to the degree of excitability of the sensory centres. Hence apparently different effects may easily be seen to be essentially only degrees of the same reaction. Thus, in one case a movement of the eyeballs or of the ear may be observed; in another this may be associated with turning the head to the opposite side. But this does not imply that in the one case I describe a motor centre for the eyeballs, and in another in the same region a motor centre of the muscles of the neck. In some cases, again, movements may be excited by stimulation of a sensory centre, apparently the same as those which result from stimulation of a truly motor centre. An instance of this will be seen on comparing the effects of stimulation of (12) in the brain of the monkey with those caused by stimulation of (14). The signification, however, is widely different in the two cases.

In the following description, in order to facilitate comparison with the results of similar experiments on the brain of the monkey, the same numbers are placed on corresponding regions. They do not pretend to indicate more than approximate physiological homologies, certain individual peculiarities being observable in different animals which scarcely admit of strict comparison with each other.

(1). On the postcrucial limb of the sigmoid gyrus.

The opposite hind leg is advanced as in walking.

There is no movement of the dog's leg comparable to that resulting from irritation of (2) in the monkey. Hence (2) is omitted in the description of the results of irritation of the dog's brain.

(3). On the first external convolution behind the crucial sulcus.

Lateral or wagging motion of the tail.

In my first experiments, as detailed in the 'West Riding Reports,' vol. iii. fig. 6, the position of the tail centre (9) was placed too far back. In the case in question the stimulation of the tail movements from so extended an area was no doubt due to a condition of hyper-excitability consequent on long-continued exploration. My subsequent experi-

ments led me to the limitation of the effective area to (3) as above.

(4). On the postcrucial limb of the sigmoid gyrus posteriorly.

Retraction with adduction of the opposite fore limb.

(5). Anterior to (4).

Elevation of shoulder and extension forwards of the opposite fore limb.

(+). Situated below (4) on the sigmoid gyrus.

In one case—a large-brained retriever—I obtained *flexion of the paw* uncomplicated with other movements. But in general when this movement was seen, it occurred in combination with the movements described under (4) and (5). The centres (6) and those marked (*a*, *b*, *c*, *d*) in the brain of the monkey are not, so far as I have found, capable of differentiation in the dog's brain.

(7). On the frontal division of the second external convolution (coronal convolution).

Action of the orbicularis oculi and zygomatics—resulting in closure of the opposite eye.

If the eyelids are forcibly kept open the eyeballs move, as has been seen also by Hitzig. The movements of the eyeballs I have found to be divergent, associated with contraction of the pupils.

(8). At the anterior conjoint extremity of the second and third external convolutions (anterior composite convolution (Langley), upper portion).

Retraction and elevation of the opposite angle of the mouth—the mouth being thus partially opened, so as to display the canine teeth.

(9). On the anterior conjoint extremities of the third and fourth external convolutions (anterior composite—lower portion).

Opening of the mouth and movements of the tongue—these movements being frequently repeated, and bilateral.

Not unfrequently stimulation of this region gives rise to barking or growling. In one case I found that each time the electrodes were placed in this region the animal uttered a loud bark. To exclude mere coincidence I shifted the elec-

trodes to various other regions, producing the actions characteristic of each as alone described; but only when the electrodes were placed on (9) was barking induced, and this with the most perfect uniformity. This region is therefore a centre of vocalisation or speech. It corresponds homologically with (9) and (10) in the monkey.

(11). On the frontal division of the third external or super-Sylvian convolution.

Retraction of the angle of the mouth.

Occasionally, especially when the frontal extremity was stimulated, the angle of the mouth was retracted on both sides, and the ear drawn forwards. This seems a more intense form of essentially the same action.

At the point marked (11′), just posterior to (11) and below (7), the action is that described under (7), viz. closure of the opposite eye.

(12). On the precrucial division of the sigmoid gyrus.

The eyes widely opened with dilatation of the pupils, with movement of the eyeballs and head to the opposite side.

In one or two instances I have seen the eyeballs converge, but in all cases the pupils were dilated.

(13). On the parietal and posterior division of the second external convolution.

Movement of the eyeballs to the opposite side, with some degree of diagonal deviation. The pupils occasionally contract, and the eyelids tend to close; though if closed at the moment of stimulation they may first open. In several instances the head moved in the same direction as the eyes.

(14). On the posterior division of the third external or super-Sylvian convolution.

Pricking, or sudden retraction, of the opposite ear.

(15). On the uncinate gyrus or extremity of the temporal lobe.

Torsion of the nostril on the same side, as if from irritation directly applied to the nostril.

Irritation of other regions of the convexity was not attended with any results altogether definite or free from complications.

Irritation of the prefrontal region sometimes causes irregular movements of the head and changes in the respiratory

rhythm, but these effects are in all probability dependent on conduction to the olfactory bulb, which lies in such close relation to this region.

On one or two occasions I observed on stimulation of the frontal division of the Sylvian convolution (16) elevation of the lip and dilatation of the nostrils; but whether these movements were due to direct irritation or conduction to the olfactory tract, which lies in immediate proximity, it was practically impossible to determine.

I have not observed any reaction on stimulation of the posterior division of this convolution. Irritation of the posterior divisions of the external convolutions has not yielded any constant results, though occasionally, especially on irritation of their mesial aspects, I have observed signs of restlessness or uneasiness, as if from painful cutaneous sensation.

Among other phenomena in connection with electrical irritation of the brain of dogs Bochefontaine[1] has described copious salivation from the submaxillary gland, as well as increase of the blood-pressure, quickening, followed by slowing, of the pulse, contraction of the spleen, intestines, and other viscera, dilatation of the pupil, and other indications of general reverberation throughout the organism. But as these effects are not associated with irritation of any one particular point, being at one time caused by the electrodes on the sigmoid gyrus and at another on some other region,[2] as well as by irritation of the dura mater or any sensory nerve, it is obvious that they are merely complications, and not the results of localised cortical stimulation.

Eulenburg and Landois[3] have observed on irritation of the motor centres of the sigmoid gyrus a slight and transient lowering of temperature in the respective limbs of the opposite side, due to contraction of the blood-vessels, the counterpart of increased temperature which follows destruction of these regions. These facts are in harmony with what is known of the correlation of vasomotor with the motor innervation of

[1] *Société de Biologie*, 1875, 1876.

[2] *Archives de Physiologie*, 1883.

[3] *Centralblatt f. d. med. Wissensch.*, 1876, and Landois' *Physiologie*, 1883, p. 799.

muscles by the researches of Gaskell[1] and others, and are what, therefore, we might have reasonably anticipated.

It has been shown by the researches of Soltmann,[2] confirmed by those of Rouget,[3] Tarchanoff,[4] and Varigny,[5] that the customary reactions of electrical stimulation are not obtainable in the brain of new-born puppies, or in the brain of new-born rabbits and other animals.[6]

It is not until after the opening of the eyes—usually about the eighth day in dogs—that the limbs can be excited to action by electrical stimulation of the sigmoid gyrus. Generally the cortical centres do not react till about the tenth day, the centres for the fore limb becoming excitable before those of the posterior limb. Similar conditions obtain in rabbits and guinea-pigs. The probable significance of these curious and apparently well-established facts will be a subject for future consideration.

Experiments on Jackals.

§ 4. The following experiments on two wild North African jackals (*Canis aureus*), which I obtained through Mr. Bartlett, superintendent of the Zoological Society's Gardens, may be taken as equivalent to those on dogs, on account of the close resemblance between these animals as to habits and as to configuration of brain (fig. 75).

(1) *Advance of the opposite hind leg* from its extended position.

(3) Some *movements of tail*, observed in the one case.

(4) *Retraction of the opposite fore leg.* In the one case this was combined with adduction, in the other the humerus was retracted and the fore arm flexed.

(5). *Elevation of the shoulder, with flexion of the fore arm*

[1] 'On the Vaso-motor Nerves of Striated Muscles,' *Journ. of Anat. and Physiol.*, vol. xi.

[2] *Jahr. f. Kinderheilkunde u. Phys. Erziehung*, 1876.

[3] *Société de Biologie*, 1875.

[4] *Revue Mensuelle de Med. et Chir.*, 1878.

[5] *L'Excitabilité Elect. des Circonvol. Céréb.*, 1884.

[6] This has however, been questioned by Paneth (Pflüger's *Archiv für Physiolcgie*, Bd., xxxvii. 1885).

and paw. This was followed by sudden extension forward. Individual centres for flexion and extension could not be differentiated in either case.

(7). *Elevation of the cheek and partial closure of the eye.* At (7′) *closure of the eye* was especially produced. The eyeballs in the one case were observed to diverge. The condition of the pupils was not noted.

(8). *The upper lip elevated and the teeth displayed,* but the mouth not completely opened.

(9). *The mouth opened and the tongue protruded.* No vocalisation was observed in either case.

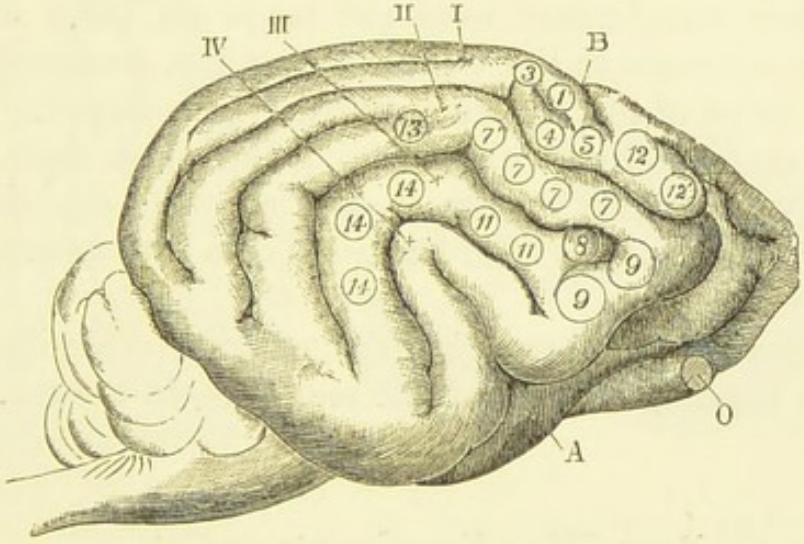


FIG. 75.—Right Hemisphere of the Brain of the Jackal.—A, fissure of Sylvius. B, crucial sulcus. I, superior external convolution. II, second external convolution. III, third external convolution. IV, fourth external convolution.—The signification of the circles and numerals is given in the text.

(11). Various points on the frontal division of the third external convolution. The *angle of the mouth strongly retracted,* the platysma being in action.

(12). *Both eyes widely opened, the pupils dilated, the eyes turned to the opposite side, the head ultimately turning in the same direction.* In the one case the eyeballs were converged, and the ears pricked up, so as to give the appearance of earnest attention.

At the anterior aspect of the same sigmoid gyrus, marked by the circle (12′), along with the wide opening of the eyes and dilatation of the pupils, the head was lowered, and the

muzzle directed to the shoulder of the same side, owing to contraction of the opposite sterno-mastoid.

(13). In the one case, and only partially explored, the stimulation of (13) caused the *head to be directed to the opposite side*, and with it the ear was pricked up, but the eyes were not observed. The pricking of the ear was like that resulting from stimulation of (14), and may have been due to a complication of the irritation of (13) with (14).

(14). *Sudden retraction or pricking of the opposite ear.* On one or two occasions the application of the electrodes in this region caused the animal to make a sudden spring or bound forward, pricking up both ears, as if suddenly startled.

Further experiments were not made on these animals, except in reference to the excitability of the posterior or recurved portion of the superior external convolution. In the one case no results were observed. In the other signs of uneasiness were caused, shown in kicking with opposite hind leg, and turning of the head backwards, as if to ascertain the cause of irritation.

In this respect the experiment agrees with a similar observation in the dog, and, as will be seen also, in the cat.

Part III.—*Experiments on Cats.*

§ 5. In the brain of the cat the convolutions are disposed in a manner similar to those of the brain of the dog and jackal.

The appearance of the brain is represented in the accompanying figures (figs. 76, 77), the one giving a surface view of both hemispheres, the other representing the left hemisphere.

The *Fissure of Sylvius* (A) and the *Crucial Sulcus* (figs. 76, 77, B) are easily recognised.

The *First External Convolution* makes a sigmoid curve round the crucial sulcus, less complex than the corresponding gyrus of the dog's brain. The *Second External* (fig. 77, II) runs parallel with the first, fusing with it posteriorly.

The *Third External* (fig. 77, III) is connected by a bridging

or *Annectent Gyrus* with the *Fourth* or *Sylvian Convolution*, which arches over the upper extremity of the fissure of Sylvius. The numeral (III) is placed on the annectent gyrus, while IV indicates the fourth external, or Sylvian, convolution.

(1). On the postcrucial limb of the sigmoid gyrus, at the upper extremity of the *ansate fissure*.

Advance of the opposite hind leg, as in walking.

(2). The homologues of (2) and (3) do not appear to exist in the brain of the cat.

(4). On the lower margin of the sigmoid gyrus posteriorly.

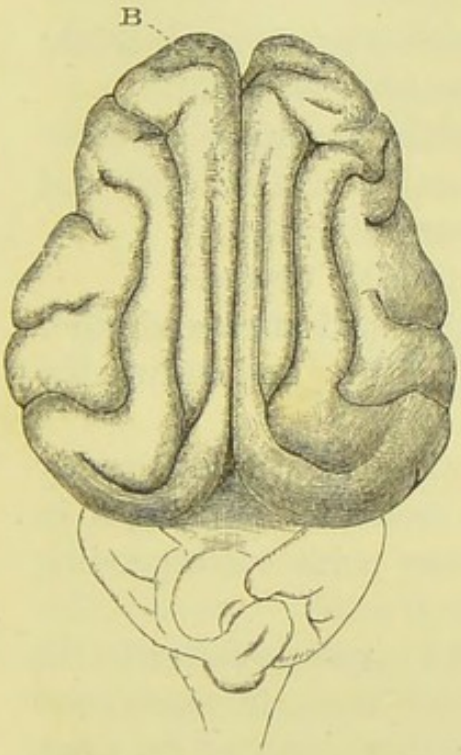


FIG. 76.—Upper Surface of the Hemispheres of the Cat.—B, the crucial sulcus.

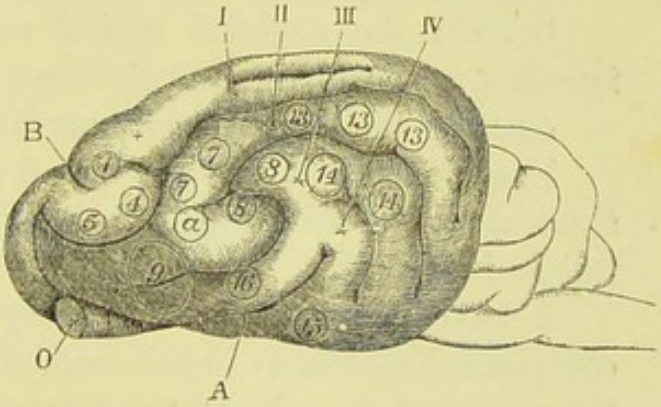


FIG. 77.—Left Hemisphere of the Brain of the Cat. A, the fissure of Sylvius. B, the crucial sulcus. O, the olfactory tract, cut. I, the superior external convolution. II, the second external convolution. III, the third external convolution. IV, the fourth external convolution.

Retraction and adduction of the opposite fore-leg. The movement performed rapidly, as it frequently is on stimulation, exactly resembles that of striking a ball with the paw.

(5). On the sigmoid gyrus anteriorly.

Elevation of the shoulder, with flexion of the forearm and paw. It would seem as if (5) and (6) in the brain of the monkey were both combined in this region.

(*a*). On the rounded frontal extremity of the joint second and third external convolutions.

Clutching or grasping action of the paw, with protrusion of the claws. This, which is one of the most characteristic actions of the cat's paw, is always very readily induced if the brain is at all excitable.

(7). On the frontal division of the second external (coronal) convolution.

Elevation of the angle of the mouth and cheek, with closure of the eye. Movements of the eyeballs were occasionally noted here both by myself and Hitzig.

(8). On the frontal division of the third external (super-Sylvian) convolution.

Retraction with some degree of elevation of the angle of the mouth, and drawing downward and forward of the ear.

Occasionally only the movement of the ear was observed.

(9). On the conjoint orbital extremity of the third and fourth (super-Sylvian and Sylvian) convolutions.

Opening of the mouth and movements of the tongue.

Frequently this was associated with vocalisation and other signs of emotional expression, such as spitting and lashing the tail as if in rage.

I have not been able to differentiate any point exactly corresponding to (11) in the dog. It seems to be included in the action of (8). Nor have I found any point corresponding to (12) in the dog and jackal.

Stimulation of the point marked (+) just posterior to the *ansate fissure*, which anatomically would seem to correspond with the tail centre of the dog, was either negative or, when the current was strong, was followed by movements of the eyes and head to the opposite side, such as occurred on stimulation of (13), the next region, due probably to diffusion.

(13). Various points on the parietal division of the second external convolution.

The eyeballs move to the opposite side, and frequently also the head moves in the same direction. The pupils were occasionally seen to contract.

(14). On the posterior division of the third external (super-Sylvian) convolution.

Pricking of the ear, and head and eyes turn to the opposite side. Sometimes only the movement of the ear occurred; and

in some cases, when the excitability of the brain was exhausted or in deep narcosis, no result whatever occurred.

(15). The tip of the uncinate gyrus.

Elevation of the lip and torsion of the nostril on the same side.

(16). On the frontal extremity of the Sylvian convolution.

Divergence of the lips, so as partially to open the mouth, which becomes fully opened when the stimulation is kept up.

In my earlier experiments I observed sudden retraction of the head on stimulation of the prefrontal regions; effects which I think are due merely to conduction of the current to the olfactory bulbs, which are in such close proximity.

Irritation of the posterior limb of the Sylvian convolution was very often associated with movements of the jaws, gene-

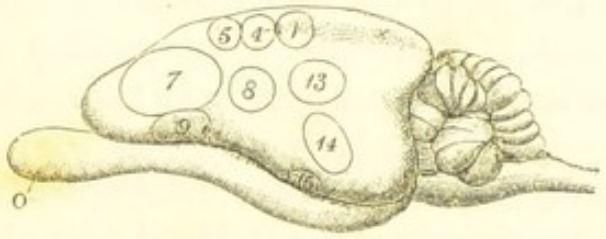


FIG. 78.—Left Hemisphere of the Brain of Rabbit.—O, the olfactory bulb. ×, para'lel sulcus. The signification of the circles and numerals is given in the text.

rally closure. Some doubts arise as to the real nature of these movements, owing to the possible conduction of the current to the cut surface of the temporal muscle, which requires to be reflected in order to reach this region.

In some experiments, just as in dogs and jackals, stimulation of the recurved portions of the first or uppermost external convolution gave rise to movements such as might be caused by painful irritation of the opposite extremities.

PART IV.—*Experiments on Rabbits.*

§ 6. The brain of the rabbit being devoid of convolutions, it is more difficult to define the exact points of stimulation. The position of the various centres was fixed in the accompanying figure by careful comparison with the dead brain during the process of experimentation (fig. 78).

A shallow sulcus (×) running parallel with the longitudinal fissure may be regarded as homologous with that marking off the superior external convolution in the dog and cat. The position of the fissure of Sylvius is indicated by a shallow depression between the narrow frontal and the broad posterior lobe, from the lower extremity of which the olfactory tract (o) is seen to spring.

(1). A point which is situated at the anterior extremity of the shallow sulcus, parallel to the longitudinal fissure.

Advance of the opposite hind leg from an extended position.

(4). *Retraction with adduction of the opposite fore limb.*

(5). *Elevation of the shoulder and extension forward of the fore limb,* as in the act of stepping forwards.

(7). Covering a large extent of the frontal aspect of the hemisphere.

Retraction and elevation of the angle of the mouth, with frequently repeated chumping or munching action of the jaws, while the head becomes gradually turned to the opposite side.

(8). Just posterior to the above mentioned.

Closure of the opposite eye, combined with elevation of the cheek and angle of the mouth, and occasionally with some undefined movement of the ear.

(9). On the orbital aspect of the frontal region.

Opening of the mouth, with movements of the tongue.

(†). I have not been able to differentiate any centres corresponding to (11) and (12) in the monkey or dog.

(13). On the parietal region.

Generally a *forward movement of the opposite eye,* and occasionally *turning of the head to the opposite side.*

In one or two instances the pupil appeared to contract, though this was regarded as doubtful.

(14) *Sudden retraction and elevation or pricking of the opposite ear*—this occasionally coinciding with a sudden start, apparently as if the animal were about to bound forward.

(15). *Torsion or closure of the nostril,* generally on both sides.

Occasionally this was associated with the movement of the ear described under (14), doubtless from conjoint stimulation of the two centres.

Stimulation of other parts of the brain gave no definite results, though in one case, on slipping the electrodes just within the longitudinal fissure posteriorly, a sudden spasmodic extension of the opposite hind leg and general shudder were produced.

Experiments on Guinea-pigs.

§ 7. The brain of the guinea-pig (fig. 79) is almost an exact copy of that of the rabbit. The results of electrical irritation are essentially the same.

The numerals have the same signification as those on the brain of the rabbit.

(1). *Advance of the hind leg.*

(5). *The fore paw is lifted* as if to step forward, and then

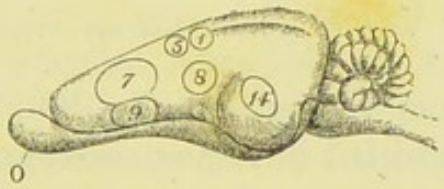


FIG. 79.—Left Hemisphere of the Brain of the Guinea-pig.—O, the olfactory bulb. The signification of the circles and numerals is given in the text.

rapidly withdrawn and adducted. The two movements of (4) and (5) in the rabbit could not be separately differentiated.

(7). As in the rabbit, *retraction and elevation of the angle of the mouth*, grinding movements of the jaws, and ultimately dragging of the head to the opposite side.

(8). *Closure of the eye and elevation of the cheek.*

(9). *Mouth opened.*

(14). *Pricking of the opposite ear.*

Experiments on Rats.

§ 8. Several experiments were made on albino rats. The results obtained were essentially the same as those in guinea-pigs and rabbits. The centres for the movements of the limbs, however, are situated nearer the frontal extremity of the hemisphere than in rabbits and guinea-pigs. The accom-

panying figures (figs. 80, 81) indicate by the same numerals the centres corresponding to those of the rabbit and guinea-pig, a separate individual description being unnecessary.

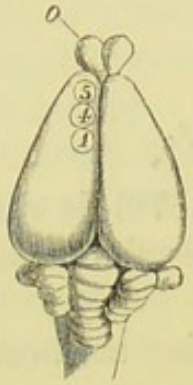


FIG. 80.—Upper Surface of the Brain of the Rat.—*o*, the olfactory bulb.



FIG. 81.—Right Hemisphere of the Brain of the Rat.—*o*, the olfactory bulb. The signification of the circles and numerals is given in the text.

PART V.—*Experiments on Pigeons.*

§ 9. The brain of the pigeon (fig. 82), as well as of the common fowl, on which I have also made experiments, though apparently constructed on the same type as the brain of rodents, differs from these in the fact that electrical irritation fails to excite analogous movements. In my first experiments

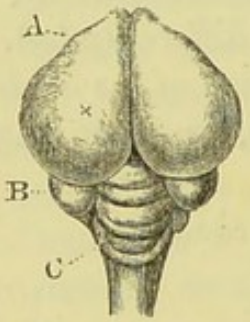


FIG. 82.—Brain of the Pigeon.

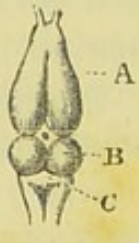


FIG. 83.—Brain of the Frog. (Enlarged × 2.)

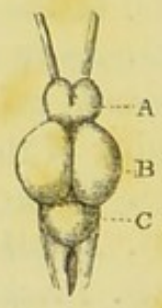


FIG. 84.—Brain of the Carp.

I had observed no result whatever on irritation of the hemisphere in any part; but in subsequent experiments I found I had missed a very definite and constant reaction, observable in connection with stimulation of a region marked on the accompanying figure (fig. 82 ×). Irritation of this point, which is situated in the upper parietal region, causes intense con-

traction of the opposite pupil, occasionally associated with turning of the head to the opposite side.

In a few cases I have also observed, from stimulation of the region below this, turning of the head to the opposite side without contraction of the pupil. Beyond these effects the results of stimulation were entirely negative.

Experiments on Frogs.

§ 10. Owing to the small size of the cerebral hemispheres of the frog (fig. 83, A), it is scarcely possible to ensure localised irritation by means of the electric current, or to avoid risks of conduction to neighbouring structures. I found, however, that the application of closely approximated fine needle electrodes to the hemisphere induced movements of the opposite limbs, but I could not differentiate regions for each limb respectively.

Langendorff,[1] who has repeated and confirmed my observations, finds that it is only from the parietal region of the hemisphere that movements can be induced by weak currents, stimulation of the other regions being ineffectual in this respect.

Experiments on Fishes.

§ 11. In fishes also the cerebral hemispheres (fig. 84, A) are relatively and absolutely of very small size, and limitation of electric stimulation correspondingly difficult. My experiments have been made on carp. I have found it comparatively easy to expose the brain and keep the animals alive during experimentation by the following method. The body of the fish was secured by a clamp fixed in a stand in such a manner as to keep the mouth just below the surface of a trough kept at a constant level by a running stream of water. Free play was allowed to the tail and fins without any alteration of position.

Irritation of the hemisphere caused the tail to be struck vigorously to the opposite side, and the pectoral, anal, and dorsal fins to be thrown into action; but their movements

[1] *Centralblatt f. d. med. Wissensch.*, 1876.

seemed too complex to admit of exact description. Generally, also, along with the movements of the tail and fins, the eyeballs moved forwards or inwards.

Part VI.—*Electrical Stimulation of the Basal Ganglia. Corpus Striatum.*

§ 12. I have found that electrical stimulation applied to the surface of the ventricular nucleus of the corpus striatum in the monkey, cat, dog, jackal, and rabbit causes precisely the same results, viz. a condition of pleurosthotonus, or general muscular contraction on the opposite side of the body. The head is drawn strongly to the side, and the body bent in the form of an arch, with the concavity to the opposite side; the facial muscles are thrown into spasmodic contraction, and the limbs are rigid in the position of equilibrium between the flexors and extensors, the flexors predominating.

In the rabbit the tonic spasm is not so rigid as in the other animals, and the jaws are ground together during the maintenance of the irritation.

There is no differentiation of movement from any point of the ventricular aspect of the ganglion, all the actions differentiated in the cortical centres being simultaneously called into play. These results have been confirmed by the experiments of Carville and Duret [1] who have found with me that general muscular contraction of the opposite side of the body occurs on the application of the electrodes to the corpus striatum.

It has, however, been asserted by Franck and Pitres [2] that neither from the corpus striatum nor from the optic thalamus is it possible to excite movements even with currents 'les plus intenses' when the electrodes are placed exactly on the ganglia themselves, whereas general muscular contraction of a tetanic character is readily induced by irritation directly applied to the internal capsule. I have, however, so often and in so many orders of animals proved the positive influence of irritation

[1] 'Sur les Fonctions des Hémisphères Cérébraux,' *Archives de Physiologie*, 2ème Série, vol. i.

[2] 'Convulsions d'Origine Corticale,' *Archives de Physiologie*, 3ème Série, vol. ii.

of the corpus striatum, and the negative influence of the same strength of current when applied to the optic thalamus, that I cannot admit the accuracy of the statements made by these physiologists. I have recently re-investigated the subject, and arrived at the same results as before on monkeys and rabbits. But in order that the results should be trustworthy it is necessary that the cerebral ventricles be exposed in such a manner as to avoid shock and hæmorrhage, otherwise no reaction will be obtained from irritation of the corpus striatum, any more than from the optic thalamus. I have generally reached the interior of the ventricles after piecemeal exposure of the hemisphere, so that sudden shock and hæmorrhage were avoided. In one instructive experiment which I recently made on a monkey I found, contrary to my usual experiences, that irritation of the corpus striatum was entirely without effect. I found, however, on further investigation, that this was due to general exhaustion of excitability, inasmuch as the corpora quadrigemina also—which usually are so readily excitable—barely reacted to an altogether disproportionate strength of current.

I am convinced that to such and similar conditions may be attributed the failure on the part of Franck and Pitres to obtain evidence of the reaction of the corpus striatum to electrical irritation.

It has, however, been proved beyond all question that the medullary fibres of the cortical motor centres are readily excitable and functionally differentiated like the centres with which they are connected. Franck and Pitres[1] have further ascertained that, on horizontal sections of the internal capsule in dogs, movements of the facial muscles, fore and hind limbs, and of the ear, can be individually elicited by stimulation of points échelonned respectively from before backwards. It is therefore not an unreasonable supposition to attribute the apparent motor excitability of the corpus striatum to actual irritation of the internal capsule by conducted currents. This mode of explanation, however, is inconsistent with other facts. If it were a mere question of conduction to the internal capsule, the same reaction should occur from the optic thalamus,

[1] *Soc. de Biologie*, Dec. 30, 1877.

between which and the lenticular nucleus the motor division of the internal capsule is situated. Conduction to the internal capsule is quite as easy in the one case as the other. But, as a matter of fact, the same current which when applied to the intraventricular nucleus of the corpus striatum produces marked pleurosthotonus is entirely without effect when the electrodes are shifted on to the optic thalamus. I have verified this repeatedly. And a statement made by Franck and Pitres themselves is sufficient to dispose of their hypothesis that the motor reactions are due to irritation of the internal capsule. They state that not even strong currents were effective when the electrodes were applied directly to the corpus striatum, while at the *same time* the fibres of the internal capsule were readily excitable by a current of much less intensity.

But inasmuch as in my own hands, as well as in those of Carville and Duret, and Minor,[1] electrical irritation of the nucleus caudatus did not fail to cause general muscular contraction on the opposite side, it is obvious conduction to the internal capsule cannot explain the results, otherwise they should have occurred under the strong stimulation employed by Franck and Pitres. The effects can only be explained on the hypothesis of direct excitability of the corpus striatum itself. Minor, however, states that after destruction of the cortical motor centres, when after the lapse of time secondary degeneration had occurred in the pyramidal tracts, he found that irritation of the corpus striatum on that side failed to excite the usual reactions; and he therefore doubts the excitability of the corpus striatum as such. But it is more probable that the tracts through which the corpus striatum acts were also involved in the degeneration, or that in the experiment in question the corpus striatum had lost its usual excitability by the operations necessary to expose it.

Optic Thalamus.

§ 13. I have not observed in the monkey, cat, dog, or jackal any outward manifestation on irritation of the ventri-

[1] 'Zur Frage ü. d. Bedeutung des Corpus Striatum' (*Neurolog. Centralbl.* June 1883).

cular aspect of the optic thalamus with a current sufficient to excite the most marked pleurosthotonus when applied to the ventricular aspect of the corpus striatum. The same negative result was obtained by Carville and Duret.

In one monkey I observed, however, a spasmodic extension of the legs on the application of the electrodes on the third-ventricular aspect of the optic thalamus in the region of the soft commissure.

In rabbits the effect of irritation of the surface of the optic thalamus was also in general without obvious result. In one case, however, I observed movements of the eyeballs, twitching of the opposite ear, shuddering and spasmodic movements of the limbs, and general restlessness during irritation of the optic thalamus; phenomena which might be manifested in connection with general sensory irritation. On no occasion did irritation of the optic thalamus, in any of the animals experimented on, cause the utterance of any sounds expressive of pain or emotion of any kind. Bechterew,[1] however, states that he has excited emotional utterance in pigeons, fowls, and dogs by mechanical as well as by electrical irritation of the optic thalami. He seems to have applied electrical irritation only by insulated needles thrust through the substance of the hemisphere to the optic thalamus.

As no such phenomena ever occurred in my own experiments in which the optic thalami were clearly exposed, I cannot accept Bechterew's statements as an accurate representation of the facts as regards irritation strictly confined to the ganglion itself.

[1] 'Die Function der Sehhügel,' *Neurolog. Centralblatt*, No. 4, 1883.

CHAPTER IX.

THE HEMISPHERES CONSIDERED PHYSIOLOGICALLY.

The Sensory Centres.

§ 1. In the preceding chapter only a bare description has been given of the phenomena of electrical irritation of the various regions of the cerebral hemispheres in different orders of animals, similar regions being designated by the same numerals for purposes of comparison. It is apparent that, with certain individual differences, peculiar to and characteristic of, the different orders of animals, there are fundamental resemblances which have an important bearing on questions of homology.

Though many of the movements described are evidently such as may be termed purposive, or combinations employed habitually for volitional purposes, there are others whose signification is not so clear; and it has still to be determined what is the real relation between excitation of a given part of the cortex and the resulting motor reactions. The mere fact of motion following stimulation of a given area does not necessarily signify a motor region. The movements may be the result of some modification of consciousness incapable of being expressed in physiological terms, or they may be reflex; or they may be truly motor in the sense of being due to irritation of a part in direct connection with the motor strands of the crus cerebri and spinal cord. The method of stimulation is by itself incompetent to decide these questions, and requires as a complement the strictly localised destruction of those areas stimulation of which gives rise to definite motor manifestations. Here, however, difficulties begin and discrepancies arise, often of the most extraordinary character. It is not such an easy matter to ensure the strict limitation of the

influence of a destructive lesion to the part immediately destroyed. For the functions of the whole nervous system, the different portions of which form a complex solidarity, may be deranged by a lesion at any part; and even if this should not be the case, there is at least great risk that the parts more immediately in relation with the lesion may be damaged temporarily or permanently. The former risk is, as a matter of fact, in experimental lesions carefully established of a very trivial character, for in the vast majority of cases the animals I have mainly experimented on, viz. monkeys, exhibit such undoubted signs of general well-being almost directly after the operation that the idea of general prostration and reverberation through the whole system requires mention only to be dismissed. The latter risk is, however, of much greater moment and reality if the animals survive the operations for many hours.

Unless the primary lesions are established in such a manner as to prevent their becoming the foci of secondary inflammatory processes, more or less diffuse, no certainty can be arrived at in respect to the direct effect of the lesions, however well anatomically circumscribed in the first instance; and thus errors of the most grievous description are apt to arise in reference to the delimitation of the respective cortical centres. The vast majority of the experiments made on this head by many physiologists, such as Munk, are vitiated by the almost universal occurrence of secondary encephalitis, with indefinite extension of the primary lesions. This, however, can be entirely obviated by the application of the Listerian principles of antiseptic surgery, such as my colleague Professor Yeo and myself have employed in our researches,[1] and adopted also by Horsley and Schäfer. By this method the absolute limitation of the primary destructive lesions can be secured without risk of secondary encephalitis or meningitis, and by this method alone is an exact delimitation of the cortical centres possible. The destructive lesions may be made with the scalpel or by means of the actual cautery, and, if the antiseptic precautions are strictly carried out, remain as exactly defined as when originally established, however long the

[1] *Brit. Med. Journal*, 1880; *Phil. Trans.* 1885.

animal may survive. A careful post-mortem examination is imperatively required in all cases, and no reliance is to be placed in merely vague statements as to the position of the primary lesion, which so many physiologists seem to think sufficient in the accounts they furnish of their experiments.

In addition to the results of physiological experiment, particularly on monkeys, which of all others have the most direct bearing on the organisation of the human brain, some reference is made in the following chapters to the facts furnished by the experiments of disease in man. These, however, require to be handled with the utmost caution, otherwise they may be made to support almost any doctrine however absurd. Almost every form of disturbance of the cerebral functions has been manifested in conjunction with anatomical lesions of the utmost diversity as to character, size, and position; and likewise without any visible or demonstrable lesion whatever. In the absence of any exact means of discrimination between the direct and indirect effects of pathological lesions, or of the relation between functional disturbance and structural alteration, little reliance can be placed on localisation of function founded on the positive facts of cerebral disease alone.[1] Clinical cases are mainly valuable as confirmatory of physiological experiments, and more especially as supplying negative instances. A case—however otherwise complicated—of total destruction of a region in which a certain function is supposed to be localised, without loss or impairment of the function assigned to it, outweighs a thousand positive instances in which a causal relationship seems to be established between the particular region and the function in question.

Part I.—*The Visual Centre.*

§ 2. The results of electrical stimulation of the occipital lobe and angular gyrus have already been recorded. No

[1] Exner's work, *Localisation der Functionem in der Grosshirnrinde*, 1881, is in many respects a typical example of the fallacies of induction *per enumerationem simplicem*. His tables and figures of 'negative instances' are, however, of great value.

appreciable manifestation was observed in connection with irritation strictly confined to the convexity of the occipital lobe, while irritation of the angular gyrus was invariably associated with movements of the eyeballs, and occasionally of the head, to the opposite side; and very frequently with contraction of the pupils. The corresponding region in the brain of the cat, dog, and jackal is the parietal aspect of the second external convolution, the posterior extremity of this being similar to the occipital lobe of the monkey in not responding outwardly to the electrical stimulus. In the brain of the rabbit the corresponding region (fig. 78, 13) likewise occupies the parietal region; and in the brain of the pigeon the centre for the contraction of the pupil (fig. 82, ×) occupies a similar position.

The phenomena of electrical irritation appeared to me indicative of the excitation of subjective visual sensation, and, acting on this hypothesis, I arrived, by the complementary method of destructive lesions, at the first delimitation of the cortical centre of vision. In my earlier experiments, owing to the complications almost invariably resulting from secondary extension of the primary lesions, if the animals were allowed to survive any length of time, I contented myself with observation of the animals for only short periods; and therefore questions were left undetermined as to the degree of permanency of the symptoms produced in the first instance. Antiseptic surgery has, however, removed the difficulties and complications formerly experienced, and the results of experiments under this method which I have since made in conjunction with my colleague, Professor G. Yeo,[1] as well as the results obtained by other physiologists, have necessitated considerable modification of the views I formerly entertained respecting the extent of the visual centres and their relations to the eyes, though the facts on which my former views were founded have been completely confirmed by my later researches.

Formerly I localised the visual centres in the angular gyri, to the exclusion of the occipital lobes. This, being only a partial truth, is an error; for the visual centres embrace not

[1] See 'On the Effects of Lesions of Different Regions of the Cerebral Hemispheres.' By Professors Ferrier and Yeo. *Philosoph. Trans.*, Pt. II., 1884.

only the angular gyri, but also the occipital lobes, which together I term the occipito-angular regions. There is, however, as will be seen, a remarkable difference between the angular gyri and the occipital lobes in their relations to the eyes. But in order to cause complete and permanent loss of vision in both eyes it is necessary completely to extirpate both angular gyri and both occipital lobes.

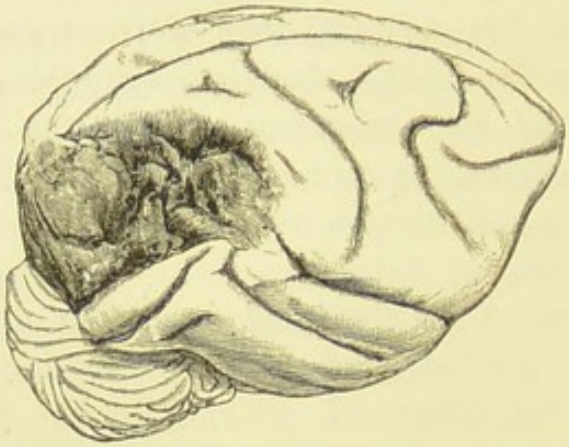


FIG. 85.—Right Hemisphere. (From a photograph.)

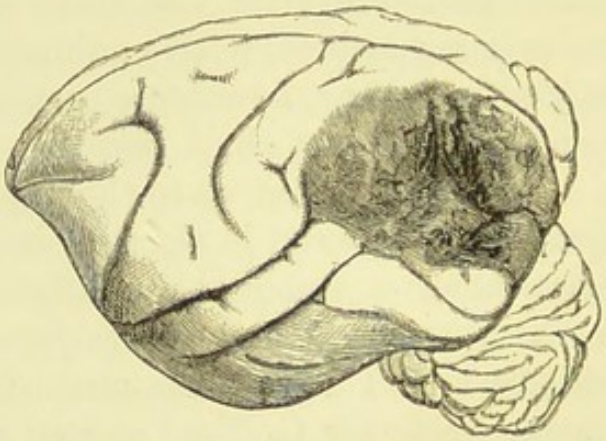


FIG. 86.—Left Hemisphere. (From a photograph.)
BILATERAL LESION CAUSING TOTAL BLINDNESS.

§ 3. In the following experiment[1] (figs. 85, 86) this operation was successfully carried out, and, as proved by careful post-mortem examination, without any secondary inflammation or extension of the primary lesion. The result of this lesion was complete and permanent blindness—for the eleven months which the animal lived—followed by atrophy of the optic discs

[1] Experiment 12*, *ibid.*

and fixity of the pupils—all other sensory faculties and the motor powers remaining absolutely unimpaired from first to last. At first the animal was unwilling to move spontaneously, as it knocked its head against every obstacle in its way. Food had to be put in its hands, as it could not find anything by itself; but it learnt to find its food by groping, and gradually gained sufficient confidence to wander about its cage and in its confines, guided by touch and hearing, which were evidently acute and perfect. It walked about with a somnambulistic air, looking apparently in the distance, and picked its way very carefully, unless startled, when it would bounce in full career against any obstacle in its way. Judging by the signs of satisfaction which it exhibited when certain articles of food—oranges, &c. —were given it, it enjoyed the sense of taste; and the manner in which it smelt at its food before eating showed that the sense of smell was retained intact. With the exception of blindness, which was from the first absolute, the animal was in complete possession of all its other faculties.

That the lesion in this case did not invade a larger area than that devoted to vision will become manifest as we proceed.

§ 4. Though the occipital lobes are included in the visual centres, it is nevertheless a remarkable fact that they can be injured, or cut off bodily, almost up to the parieto-occipital fissure, on one or both sides simultaneously, without the slightest appreciable impairment of vision. This fact, which I had already observed in my former experiments, has been completely confirmed by Professor Yeo and myself, and also by Professors Horsley and Schäfer. The statements of Munk,[1] that lesion of one occipital lobe causes hemianopsy towards the opposite side, by paralysis of both retinæ on the side of lesion, and that bilateral lesion causes complete blindness, are entirely erroneous, and depend on direct implication or secondary extension of the lesion into the angular gyri. In two cases[2] I removed the greater portion of both occipital lobes at the same time without causing the slightest appre-

[1] *Die Functionen der Grosshirnrinde*, 1877–1880, Berlin, 1881.

[2] Experiments XXII. and XXIII., *Philosoph. Trans.* vol. clxv. Part II., 1875 (figs. 29–34).

ciable impairment of vision. One of these animals (fig. 87) within two hours of the operation was able to run about freely, avoiding obstacles, to pick up such a minute object as a raisin without the slightest hesitation or want of precision, and to act in accordance with its visual experience in a perfectly normal manner.

In another animal[1] in which (fig. 88) both occipital lobes had been likewise removed, and which survived for nearly a month when the prefrontal lobes were also removed, there was from the first some slight visual disturbance, evidenced by

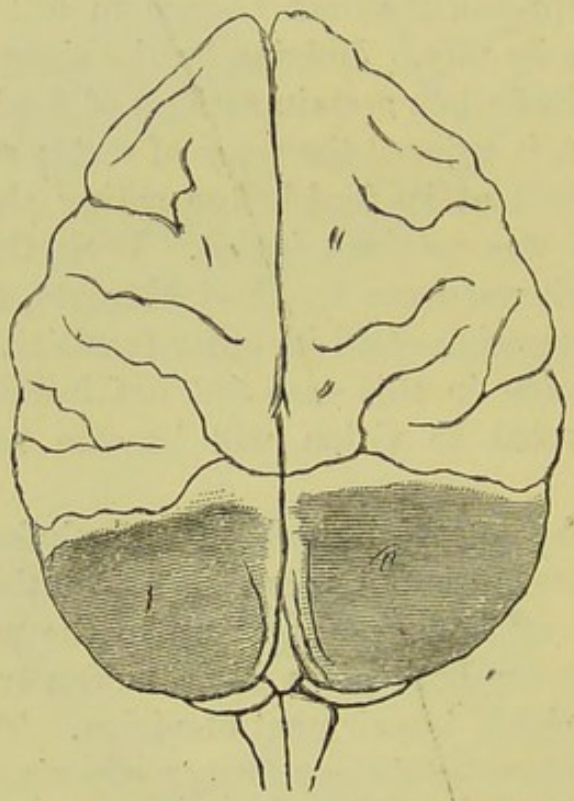


FIG. 87.—Lesion of both Occipital Lobes. (Roy. Soc.)

some want of precision in laying hold of things offered it; but it was found on post-mortem examination that the right angular gyrus was injured as well as both occipital lobes.

In another experiment,[2] in which both occipital lobes and both angular gyri were implicated, blindness was observed during the two days which the animal survived. In all cases in which there was impairment of vision the lesions invaded also the angular gyrus on one or both sides.

[1] Experiment XXIV., *Phil. Trans.* vol. clxv. Part II. figs. 35-37.

[2] Experiment XXI., *ibid.* figs. 26-28.

Among the monkeys operated upon by Dr. Yeo and myself one[1] had the left occipital lobe severed and removed closely behind the parieto-occipital fissure without any perceptible affection of vision to the one side or the other, the animal being able to see and seize things both to right and left. In another,[2] both occipital lobes were deeply incised and broken up without the slightest impairment of vision. And in a third[3] both occipital lobes were removed so extensively as only to leave a triangular portion of each behind the upper extremity of the parieto-occipital fissure.

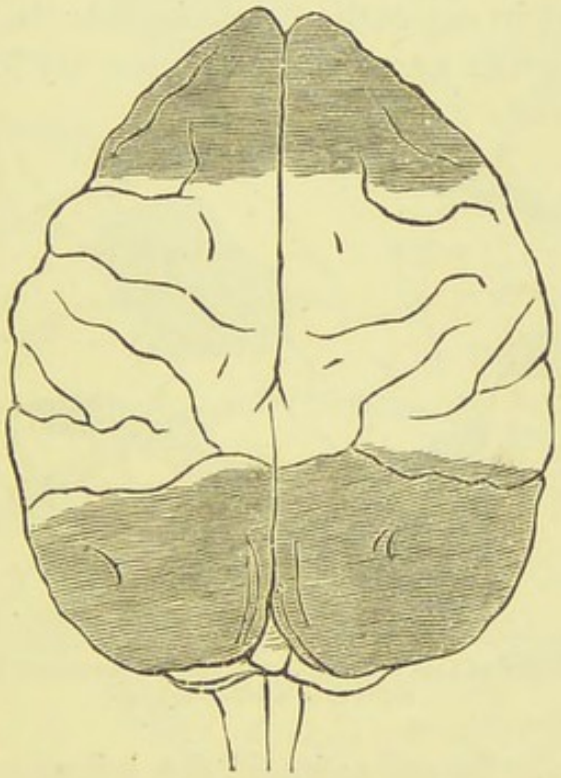


FIG. 88.—Removal of Occipital and Prefrontal Lobes. (Roy. Soc.)

Yet this animal within two hours after the operation was able to run about freely, pick up minute objects, and in general, from this time onwards, to behave as if nothing whatever had occurred to it. Its powers of vision showed no signs of impairment, and it exhibited no defect as regards general intelligence.

[1] Experiment 1 *, *Phil. Trans.* Part II., 1884, fig. 1.
[2] Experiment 2 *, *ibid.* figs. 2 and 3.
[3] Experiment 9 *, *ibid.* fig. 15.

Horsley and Schäfer inform me[1] that the results of removal of the occipital lobes in their experiments entirely harmonise with mine as to the completely negative effect of this operation on the animal's visual and other faculties.

We can therefore dismiss Munk's statements as to the effects of lesions of the occipital lobes as being unfounded and erroneous.

§ 5. But when we turn to the effects of destructive lesions of the angular gyrus unilaterally and bilaterally, and to these in combination with lesions of the occipital lobes, very remarkable relations are found to exist.

I had found in my earlier experiments that a destructive lesion of one angular gyrus caused temporary loss of vision in

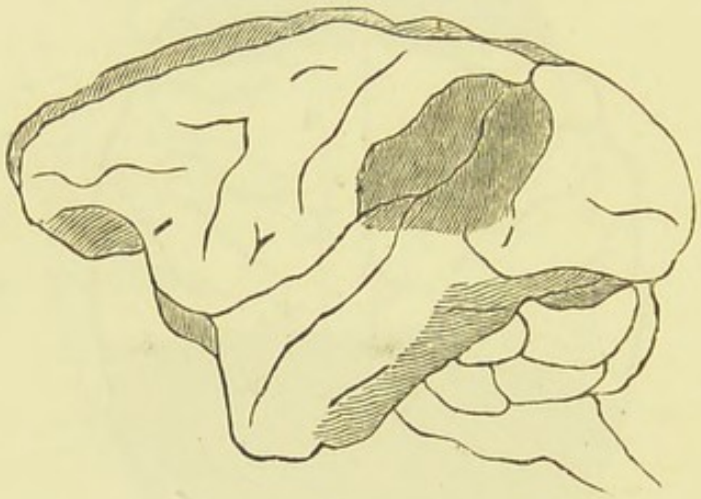


FIG. 89.—Destruction of Left Angular Gyrus, causing temporary blindness of the right eye. (Roy. Soc.)

the opposite eye. In one animal[2] the left angular gyrus was destroyed (fig. 89), and the left eye securely closed. After recovery from the chloroform stupor the animal began to grope about a little, but would not budge from its position, though it was evidently on the alert and in full possession of its other faculties.

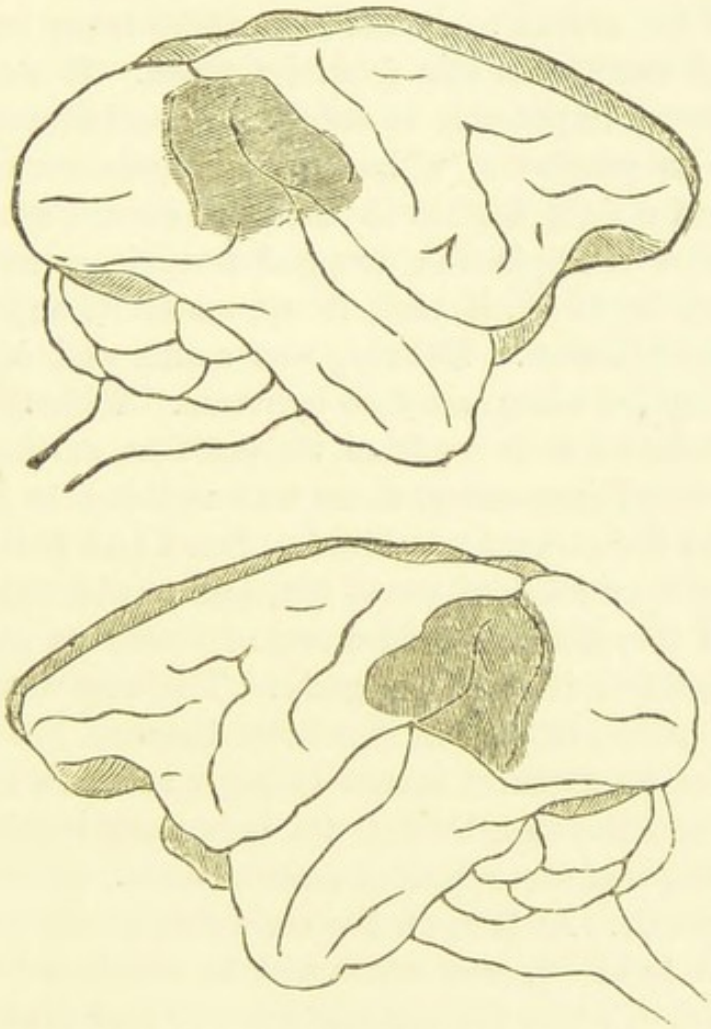
It did not flinch at light flashed in its eyes. After it had remained in this condition for an hour the bandage was removed from the left eye, whereupon the animal nimbly made off, and ran through the open door of its cage to join its com-

[1] Private communication.

[2] Experiment VII., *Phil. Trans.* vol. clxv. Part II., 1875, fig. 9.

panions. Next day when the left eye was again bandaged no affection of vision could be discovered in the right eye.

In another case[1] in which previously the motor centres of the left hemisphere had been destroyed, with the effect of causing right hemiplegia, the angular gyrus was destroyed. This was followed by temporary total loss of vision in the right eye, so that the animal, when obliged to move, which it



FIGS. 90 and 91.—Bilateral Lesion, causing temporary complete loss of vision.

did very unwillingly, ran its head full tilt against everything that came in its way. The removal of the bandage which had been put on the left eye was followed by an instantaneous transformation, and the animal began to run about and act as if suddenly restored to the enjoyment of sight. In a third[2] similar experiment the results were exactly the same. In a

[1] Experiment VIII., *op. cit.* fig. 10. [2] Experiment IX., *op. cit.*

fourth experiment [1] the angular gyrus was exposed and accurately destroyed with the galvanic cautery in *both hemispheres*.

Before this was done the animal had been allowed fully to recover from the narcosis under which the operations of exposing the angular gyri had been effected. When it had been satisfactorily determined that vision was perfect, the angular gyri were seared with the cautery without further narcotisation, and without the slightest sign of pain or discomfort on the part of the animal. It was at once let loose, but appeared scared, and would not stir from its place. It was therefore for some hours impossible to obtain any satisfactory information as to its powers of vision. The pupils were contractile to light, and a light flashed in the eyes caused some wincing. When a piece of apple was dropped near it, so as to come in contact with its hand, it took it up, smelt it, and ate it with signs of satisfaction. Hearing was acute, and it turned its head and replied when called to by name. With the exception of the reluctance to move from its position, arising evidently from a sense of insecurity, there was nothing to indicate decisively that the animal was blind. But I had found that this animal was very fond of sweet tea, and would run anywhere after it. I therefore brought a cup of sweet tea and placed it to its lips, when it drank eagerly. The cup was then withdrawn and placed in front of it, a little distance, but the animal, though from its gestures intensely eager to drink further, was unable to find the cup, though its eyes were looking straight into it. This test was repeated several times, and with exactly the same result. At last, on the cup being placed to its lips, it plunged its head in, and continued to drink till every drop was exhausted, while the cup was lowered and drawn half-way across the room. Next day the animal still continued blind, and paid no attention to threats, grimaces, or other means of appeal to its sense of vision. The animal was then killed in order that the position and extent of the lesions might be accurately determined before secondary inflammatory processes could have advanced. These had already begun, but were confined to the angular gyri, which were somewhat swollen and raised, and to the adjoining anterior margin of the occipi-

[1] Experiment X., *op. cit.*

tal lobes, and with slight implication of the posterior margin of the left ascending parietal convolution. The destruction was purely cortical, the grey matter alone being disorganised, and in the angular gyri exclusively (figs. 90, 91).

These facts seemed to justify the opinion I expressed that the angular gyri were the centres of vision, each being in complete cross relation with the opposite eye, since the effect of unilateral extirpation was evidently for the time total blindness of the opposite eye, and not hemiopia. And it further seemed as if the rapid recovery from unilateral lesion were due to the compensatory action of the other gyrus, inasmuch as bilateral destruction caused total blindness in both eyes of a more enduring and, as I ventured to suppose, probably permanent nature. But further investigation, on animals which have been permitted to survive for much longer periods than were compatible with exact experiments under old surgical methods, has shown that the visual centres of the cortex are of a much more extensive character. In my first experiments antiseptics were not used, and hence some degree of inflammatory action and consequent disturbance of the grey matter immediately in relation with the actual lesion were unavoidable, even though not obviously perceptible to the eye for some hours after the operation. In my later researches with Professor Yeo, in which stringent antiseptic precautions were employed, secondary extension of the primary lesions was entirely prevented, and the duration of the total loss of vision in the opposite eye after lesion of the angular gyrus, if the lesion were superficial, was found in several instances to be even more transient than I had previously found to be the case; while the effects of bilateral lesions were found to vary according to whether they were established simultaneously or successively.

In one case[1] destruction of the convexity of the right angular gyrus was found to cause some imperfection of vision —shown in an incorrect appreciation of the distance of objects when both eyes were open—which proved, on the right eye being bandaged, to be due to total blindness in the left eye, so that the animal refused to stir, or, if it did so on compul-

[1] Experiment 3*, *Phil. Trans.*, vol. ii. 1884. fig. 4.

sion, ran against every obstacle in its path. On the bandage being removed from the right eye, after a short period of observation, the animal speedily showed that it was able to direct its movements with perfect precision. These observations were made within the first two or three hours after the operation, and next day no trace could be discovered of the symptoms.

Though it has been urged by some, against the validity of this and other experiments to be recorded, that the observations were made while the animals were still in a state of stupor or shock following the operation, this is false, for no observations were made until the animals clearly showed perfect possession of all their other faculties. The period of reliable observation is not to be measured by the mere time that has elapsed since the operation, for the period of recovery is most variable, many animals being up and active almost before their wounds have been dressed. Those who do not take advantage of the earlier opportunities of observation miss important facts which are beyond all possibility of question.

In another animal,[1] destruction of the convexity of the left angular gyrus was followed by total blindness of the right eye, so that for the three hours it was observed after full recovery of all its other faculties it ran against every obstacle right and left, and failed to respond to any test of vision that could be devised. Next day, the left eye being still bandaged, it showed to all appearance the possession of perfect vision with the eye which was totally blind the day before. Three weeks subsequently the right angular gyrus was similarly destroyed by the cautery, whereupon the animal became for a time totally blind in both eyes ; being unable to move about without knocking against obstacles, and paying no attention to signs and tests, which would certainly have called forth response in a normal animal. At the end of two or three hours it began to give some indications of returning vision, and next day appeared quite well and in full enjoyment of its visual faculties.

In this case the destruction of the other angular gyrus had re-induced the blindness in the eye, which had apparently

[1] Experiment 5*, *Phil. Trans.*, vol. ii. 1884, fig. 7.

quite recovered its powers, indicating a bilateral relation between each angular gyrus and the eyes.

In another case[1] destruction of the convexity of the left angular gyrus was followed by similar temporary total blindness in the right eye, which next day had entirely disappeared; but on lesion of the right angular gyrus three weeks afterwards vision became temporarily impaired in the right eye, the one which had been affected previously, while no apparent defect could be discovered in the opposite eye. This occurrence was unusual, and careful examination was made as to whether the defect was of a hemiopic nature, but it was perfectly clear to rigid tests that neither after the first nor second operation was the defect to one side or the other, but purely of an amblyopic character. The lesion of the right angular gyrus was less extensive than that of the left. Yet the condition was such as to show again a bilateral relation of the angular gyrus, the second operation showing itself mainly, if not entirely, in the eye which had already been blind temporarily by reason of destruction of the opposite angular gyrus. In this animal, at a subsequent date, the lesions of both angular gyri were extended backwards in a third operation into the anterior margins of the occipital lobes across the parieto-occipital fissures. This operation was so entirely negative that the animal was found running about the room as if nothing had happened to it within fifteen minutes after the completion of the operation. It continued in perfect health and in full enjoyment of all its faculties till it was killed by chloroform four months afterwards; a striking example of the safety of even repeated operations on the brain and its membranes under strictly antiseptic precautions.

In another animal[2] in addition to the destruction of the convexity of the left angular gyrus, the corpus callosum was torn through posteriorly, with a view to determine whether the rapidity of compensation of a unilateral lesion depended on the integrity of the corpus callosum. It had already been determined by a special experiment[3] that division of the

[1] Experiment 4*, fig. 4, *Phil. Trans.*, vol. ii. 1884.
[2] Experiment 7*, figs. 9–11, *ibid.*
[3] Experiment 6*, fig. 8, *ibid.*

corpus callosum had no paralysing effect either on the motor or sensory faculties. After the lesion in question the right eye was totally blind for several hours, but next day the animal was able to run about in every direction with perfect vision on all sides in the eye which had been totally blind the day before. The lesion of the corpus callosum had therefore no influence on the rapidity of compensation. When five weeks subsequently the right angular gyrus was injured, but to a less extent than the left, total obscuration of vision in both eyes occurred, but of the most transient duration. On the right eye being bandaged, marked impairment of vision was evident in the left eye on all sides; but this also speedily disappeared, and the animal remained perfectly well, and in full enjoyment of vision and all its other faculties.

In another animal[1] both angular gyri were cauterised very thoroughly, so as to destroy the grey matter of the sulci as well as the convexity. Total blindness ensued in both eyes without other defect, sensory or motor. The total blindness continued, however, only for three days. On the fourth day some indications of returning vision were observed, but the animal never during the whole period of its survival—over two months—regained perfect vision, but always exhibited some uncertainty or want of precision in its endeavours to seize things offered it, or to pick up minute articles of food from the floor, such as currants or grains of corn.

After death it was found that the angular gyri had been completely obliterated; but the occipital lobes and the optic radiations (fig. 25, *or*) passing backwards into them were uninjured. A suggestion has been made that injuries of the angular gyrus affect vision only by reason of implication of the optic radiations of the occipital lobes; but this has no foundation in actual fact. Nor, if it were, would the result be cross amblyopia, but homonymous hemiopia towards the opposite side, in case of unilateral lesion, and total and permanent blindness in case of bilateral destruction of the tracts in question. The above-mentioned experiments show that lesion of the angular gyrus in all cases causes impairment of vision more or less transient according to the extent of the

[1] Experiment 8*, figs. 12–14, *Phil. Trans.*, Part II., 1884.

injury. The affection is not of a hemiopic nature, but shows itself in total blindness or amblyopia of the opposite eye. But the rapidity of compensation, and the fact that subsequent destruction of the other gyrus affects the clearness of vision in both eyes, indicate that each angular gyrus has relations with both eyes, though the cross relation is the only perceptible one on unilateral lesion. The last-mentioned experiment renders it doubtful whether complete clearness of vision is ever regained after total extirpation of both angular gyri.

§ 6. As to other effects of lesion of the angular gyrus I have never seen, either on unilateral or bilateral destruction, the slightest appearance of ptosis or paralysis of the ocular muscles; and, in direct contradiction to Munk, I have found the sensibility of the conjunctiva and the reflex closure of the eyelids as distinct as in the normal condition. If one may utilise Munk's own data, the account he gives of the effects of lesion of the angular gyrus demonstrates the absurdity of his notion that the angular gyrus is the sensory centre of the eyeball, and confirms the account above given of its relation to vision.[1] After destruction of the left angular gyrus he found that brusque approximation of the finger to the left eye invariably caused winking, but the same action against the right eye only caused winking when the eyelids were actually touched; a clear proof of the sensibility of the eye, and the non-perception of the threatened danger at a distance. This absence of winking at threatened danger he admits to be characteristic also of true blindness; but inasmuch, says he, as this animal could not be blind, presumably because its occipital lobe was intact, 'therefore the absence of winking could only be due to the inability of the cortex to act on the sphincter palpebrarum.' This exquisite specimen of *petitio principii* needs no further comment. Further, he says that after destruction of the left angular gyrus, and closure of the left eye, the animal often fails to seize things offered it, or thrown down before it, especially when the objects are small—another clear indication of defective vision. Lastly, he says that on bilateral extirpation of the angular gyrus he has observed that monkeys 'after incomplete restitution'—whatever

[1] Munk, *Die Functionen der Grosshirnrinde*, p. 64.

this may mean—are unable, like normal monkeys, to take things offered them delicately with the fingers, but instead make grabs at them with the whole palm. This is only a further illustration of the same imperfection of vision observed in the last-mentioned experiment, which consisted in a want of precision in prehension, and a continual tendency to place the hand over, to the side, or short of, the object wished for, instead of directly on it at once.

§ 7. We have seen that the occipital lobes may be removed without any appreciable impairment of the faculty of clear vision; that unilateral destruction of the angular gyrus produces only transient loss of vision in the opposite eye; and that even bilateral destruction of the angular gyrus does not cause permanent total loss of vision. When, however, the angular gyrus and occipital lobe are together destroyed in the one hemisphere, as in the following experiment, transient amblyopia occurs in the opposite eye, and more or less enduring hemiopia in both eyes towards the side opposite the lesion, by reason of paralysis of both retinæ on the side corresponding to the lesion. This condition of hemiopia, first pointed out by Munk, has been erroneously attributed by him to lesion of the occipital lobe alone, owing to the imperfection of his experimental methods.

In the case in question[1] the convexity of the left angular gyrus, together with the whole convex aspect of the left occipital lobe, was destroyed with the galvanic cautery. Transient total blindness occurred in the right eye, so that the animal continued for an hour to knock its head against every obstacle, and to be irresponsive to every test of vision. Subsequently, however, it was found, on examination of the right and left eye respectively, that there was loss of vision towards the right side. The animal knocked the right side of its head when moving among obstacles, and took things offered it, or picked up objects from the floor, only towards the left. In this animal, however, the hemiopia was not permanent, and within the short space of a fortnight all traces of the defect, formerly so evident, had disappeared. In this case, however, portions of the angular gyrus and a considerable portion of

[1] Experiment 10*, fig. 17, *Phil. Trans.*, Part II., 1884.

the mesial and inferior aspect of the occipital lobe remained intact.

In another animal[1] a kind of diagonal experiment was performed. The convexity of the left angular gyrus was first destroyed. Vision in the left eye appeared unimpaired. Vision with the right eye was lost, or impaired; but within an hour and a half the animal could see sufficiently well with this eye as to be able to pick up small articles of food on either side indifferently. Four months subsequently—the animal in the meantime being in all respects perfectly well—the right angular gyrus was cauterised, and the right occipital lobe removed bodily. The result of the second experiment was hemiopia towards the left. Repeated tests of the range of vision in the right and left eye respectively proved that the limitation of vision was much greater in the left than in the right eye, the animal with the left eye closed being able to see well to the right, and also considerably to the left of the median line; while with the right eye closed vision to the left of the middle line appeared completely lost. As time went on, the range of vision to the left gradually increased, until, within a month after the second operation, it was impossible to discover in the manner in which the animal used its hands and eyes any sign of the hemiopic defect previously so manifest.

In this case post-mortem examination proved that the left angular gyrus was merely superficially eroded, while the occipital lobe was intact; while on the right the convexity only of the angular gyrus was destroyed, but the occipital lobe was obliterated. Yet, notwithstanding this extensive bilateral destruction of the visual centres, vision was ultimately regained to such an extent that no appreciable defect could be discovered in the animal's powers of visual perception and ideation.

A somewhat similar diagonal bilateral lesion was made in the case of a monkey previously referred to (p. 275).[2] Both occipital lobes had been extensively destroyed without any perceptible impairment of vision. Six weeks subsequently

[1] Experiment 11*, fig. 16, *Phil. Trans.*, Part II., 1884.

[2] Experiment 9*, *ibid.*

the left angular gyrus was cauterised on the convexity, with the effect of causing temporary blindness in the right eye. This within a few hours had so far disappeared that the animal was able to guide its movements and pick up grains of oats from the floor with precision towards the left, but with some uncertainty towards the right. Next day clear vision to the right as well as to the left was fully established; and from this time onwards no defect could be discovered. The animal continued active, vivacious, and intelligent, and maintained the leadership of its companion monkeys, which it had previously assumed.

Though, therefore, after extensive destruction of the occipito-angular region in one hemisphere, the temporary amblyopia of the opposite eye leaves a more enduring homonymous lateral hemiopia to the opposite side, yet unless the destruction of the cortex in this region is absolutely complete (and in none of the above-recorded experiments was this the case) restoration occurs, to such an extent at least that the defect ceases to be perceptible by any tests applicable to the lower animals. Whether exact perimetric exploration, such as can be carried out on human beings, would reveal some defect of visual acuity towards the opposite side is not improbable; but the facts show beyond doubt that the previous total hemiopia gives place to such a restoration of vision that the animal becomes again able to direct its actions with intelligence and precision accordingly. Luciani and Tamburini[1] have also found that the hemiopia, at first evident after destruction of the angular gyrus and portion of the occipital lobe, is only of temporary duration.

But there are reasons for believing that the restoration is due to incomplete destruction of the visual centres on the one side, and that hemiopia persists if every portion of the centres is removed or destroyed. It is, however, extremely difficult thoroughly to destroy a given centre, if at all extensively convoluted, by pure decortication, apart from secondary inflammatory action. Complete obliteration can be effected more readily, though without precision, by the secondary encephalitis usually following lesions established without anti-

[1] *Sui Centri Psico-sensori Corticali*, 1879.

septic precautions; and particularly by lesions implicating the medullary fibres of the given centre before they have radiated to their ultimate cortical terminations.

It is under the latter conditions, both in man and animals, that permanent hemiopia has been mainly, if not exclusively, observed in connection with lesions of the occipito-angular region.

In one animal,[1] while endeavouring to destroy the hippocampal region, I inflicted considerable injury on the medullary fibres and cortex of the left occipito-angular region. This resulted in some degree of right hemiopia, which, however, soon disappeared. The subsequent more extensive destruction of the optic radiations of the occipito-angular region of the right hemisphere gave rise to left hemiopia, which at the end of three months was as absolute as at first, and showed no indications of retrogression. In this case the damage to the visual centres of the left hemisphere may have prevented their compensating for the lesion in the right hemisphere, if that were possible; but the facts of clinical medicine are sufficient to prove that similar lesions confined to the one hemisphere are capable of causing permanent paralysis of the corresponding sides of both retinæ.

§ 8. The various facts above narrated show that each hemisphere is in relation with the corresponding half of both retinæ, and that the semidecussation of the optic tracts, previously demonstrated (Chapter V. § 3) is maintained in the cortical centres. But the retinal relations of each hemisphere are somewhat more complex than a simple division of the retinal fields into two correlated halves projected on the corresponding side of each hemisphere. For we have seen that unilateral lesion of the angular gyrus produces a temporary blindness, or amblyopia, of the opposite eye, which has none of the characters of hemiopia; and bilateral destruction induces a more or less permanent impairment of visual acuity on both sides. Certain facts recorded serve to show that each angular gyrus has relations with both eyes, inasmuch as injury of the second, some time subsequently to the apparent entire disappearance of the effects of the first lesion, induces defect

[1] Experiment 26, figs. 117-124, *Phil. Trans.*, Part II., 1884.

in both eyes. The cross action is, however, the only one which is capable of being detected in the lower animals from unilateral lesion; though this does not exclude the possibility of a slighter impairment of vision in the eye of the same side, not perceptible to ordinary tests.

It appears to me, therefore, that, in addition to the representation of the correlated halves of both retinæ in the corresponding occipito-angular region, the angular gyrus is the special region of clear or central vision of the opposite eye, and perhaps to some extent also of the eye on the same side. We have seen that the removal of the occipital lobes does not appreciably impair the faculty of vision, but that in all cases disturbances of vision, however temporary, resulted from lesions of the angular gyri alone. With these facts also should be taken the results of electrical exploration of the visual centres. While irritation of the angular gyrus invariably caused movement of the eyeballs to the opposite side, irritation of the occipital lobe was uniformly negative.[1] As these as well as certain other movements above described (Chapter VIII., § 6) are most probably merely associated movements, indicative of subjective visual sensations, their excitation from the angular gyrus alone would support the view that this is the centre of clearest vision.

Before satisfactory evidence had been adduced to prove that hemiopia might occur in man in connection with cortical or subcortical lesions in the posterior lobe, Charcot, founding mainly on the facts of hysterical hemianæsthesia, had come to the conclusion that lesions of the hemisphere, or of the posterior division of the internal capsule, produced only cross blindness or amblyopia of the opposite eye. In order to account for this phenomenon, and at the same time to explain the hemiopia resulting from direct lesion of the optic tract, he propounded the following scheme of the constitution and relations of the optic tracts (fig. 92, with description).

Among the fibres of the chiasma are some (b' a) which cross to the opposite eye, and others (a' b) which pass to the

[1] Luciani and Tamburini (*op. cit.*) have observed similar movements also from irritation of the occipital lobe. In reference to this I can only say that my explorations on at least ten separate animals gave no such phenomena.

eye of the same side. The latter lie externally, while the former occupy a more central position in the optic tracts. Each tract in fact contains fibres for each eye, the external for the eye on the same side, the internal for the corresponding half of the opposite eye. Hence lesion of the left side of the chiasma, or of the left optic tract (K), will cause hemiopia of both eyes, paralysing the left side of both retinæ.

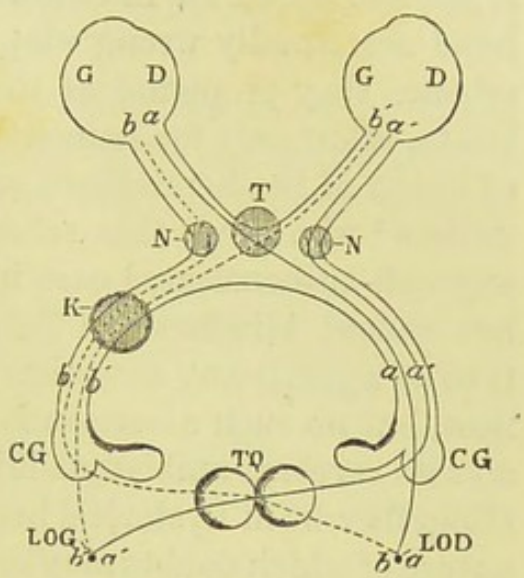


FIG. 92.—Scheme of the Decussation of the Optic Tracts, according to Charcot.—T, semi-decussation in the optic chiasma. TQ, decussation posterior to the corpora genicu'ata. CG, corpora geniculata. *a'b*, fibres which do not decussate in the chiasma. *b'a*, fibres which undergo decussation in the chiasma. *b'a'*, fibres coming from the right eye which meet in the left hemisphere LOG. LOD, right hemisphere. K, lesion of the left optic tract, producing right lateral hemiopia. LOG, a lesion at this point, producing right amblyopia. T, lesion producing temporal hemiopia. NN, lesion producing nasal hemiopia.

The external fibres, or those which do not decussate in the chiasma, decussate with their fellows in the corpora quadrigemina (T Q), and so reach the opposite hemisphere; while the fibres which decussate in the chiasma do not again decussate in these ganglia, but pass directly through the corpora geniculata (C G) into the hemisphere (L O G, L O D). In consequence of this arrangement all the fibres of the right eye reach the left hemisphere, and all those of the left eye the right hemisphere.

Hence lesion of the cerebral centre causes complete blindness of the opposite eye; while lesions lower down, whether in the corpora quadrigemina, corpora geniculata, or optic tracts, affecting the two sets of fibres before they have run their complete course, cause partial blindness, or hemiopia of each eye.

It cannot, however, be doubted that this scheme is unsatisfactory, and in contradiction with now well-established clinical, as well as experimental, facts, which prove that hemiopia may result from cortical and subcortical lesions of the posterior lobe, not affecting the optic tracts. Landolt[1] has also shown that, even in those cases in which apparently only

[1] *La France Médicale*, Feb. 3, 1877.

the opposite eye is affected, there is also some contraction of the visual field in the eye of the same side; a condition which is not accounted for in Charcot's scheme. Those on the other hand are equally wrong who, like v. Gräfe [1] and Féré,[2] in the scheme they propound of the cortical relations of the optic tracts, allow only for homonymous hemiopia as a consequence of lesion of the hemisphere or internal capsule. Some of the writers [3] who adopt this scheme boldly deny the existence of any well-authenticated case in which lesion of one hemisphere has caused blindness in the opposite eye. This is perfectly true as against any assertion of permanent monocular blindness, but no such assertion is made by those who contend that a cross cerebral amblyopia is both possible and proved. Apart altogether from hysterical hemianæsthesia, respecting the true nature of which doubts may be entertained,[4] there are on record [5] several carefully investigated cases of hemianæsthesia, due to organic disease, in which, with some degree of contraction of the visual field of the eye on the same side, there has been almost complete blindness, or very great impairment of vision, in the opposite eye.[6]

[1] *Gaz. Hebdomad.* 1860. [2] *L'Hémianopsie*, 1882.

[3] Mauthner, *Vorträge a. d. Gesammtgebiete der Augenheilkunde*, 1881; Starr, 'The Visual Area in the Brain, &c. *Amer. Journ. Med. Sci.*, 1884.

[4] A hypothesis of, in my opinion, a very far-fetched character has been propounded by Priestley Smith ('Reflex Amblyopia,' *Ophthal. Review*, May 1884) in explanation of the amblyopia met with in hysterical hemianæsthesia. This is to the effect that the amblyopia is due to reflex contraction of the vessels which nourish the retina. Though a general ischæmia exists on the hemianæsthetic side, this is only one of an assemblage of correlated phenomena; and to make it the cause of all the others, and to attribute to a degree of ischæmia, which is not discoverable by the ophthalmoscope, not only the amblyopia, but also the deafness, loss of taste and smell, loss of motor power, and the profound hemianæsthesia which exists in these cases, is a very large assumption, and without parallel elsewhere in the whole range of pathology. Our author attempts to account for the amblyopia, which I have described in connection with lesion of the angular gyrus, by a reflex contraction of the retinal vessels, caused by the cerebral injury. A reflex action from irritation of an insensitive surface would be a further novelty in physiology and pathology. And even if it could be admitted, the fact that it only occurs from lesion of the angular gyrus would show that this region has a special relation to the eye of the opposite side.

[5] Grasset, *Montpellier Médical*, 1883; Ferrier, 'Cerebral Amblyopia and Hemiopia,' *Brain*, Part XII., 1881.

[6] Sharkey (*Medico-Chir. Transactions*, vol. lxvii. 1884) has recorded a case

To such conditions the term hemiopia is altogether inapplicable, and the schemes of the constitution and relations of the optic tracts constructed by v. Gräfe and his followers fail to explain them satisfactorily.[1]

Of the various diagrams representing the relations of the optic tracts the one suggested by Sharkey[2] most nearly accords with experimental and clinical facts; but it fails to account

of great importance in this relation. The patient, a woman, aged 41, died in St. Thomas's Hospital of cardiac and pulmonary disease. Seven years previously she was admitted as a patient into Guy's Hospital suffering from left hemiplegia and hemianæsthesia. At this time there was dimness of vision in the left eye almost amounting to complete blindness. Four weeks after the onset of the attack vision in the left eye had greatly improved, along with the other forms of sensation of the left side; and, after less than three weeks more, vision in the left eye was completely restored.

From this time till her death some degree of left hemiplegia continued, but the hemianæsthesia had disappeared, and vision with the left eye was perfectly normal, there being no hemiopia or colour-blindness. The cause of the left hemiplegia and anæsthesia was an embolism of the right middle cerebral artery, leading to softening and absorption of a considerable area of the left hemisphere, including the angular gyrus. But the occipital lobe was intact and in nowise reduced as compared with the right.

Though, in this case, the lesion was too extensive to allow of accurate localisation, and though there appears to have been no accurate perimetric investigation of the field of vision in both eyes, there can be little doubt that the affection of vision was mainly of the nature of a crossed amblyopia, such as results from lesion of the angular gyrus in the monkey. And it is further noteworthy that the occipital lobe was uninjured.

It is quite true that patients affected with hemiopia complain mainly, not exclusively, of loss of vision in the eye on the hemiopic side. Thus an individual with loss of vision towards the right, owing to homonymous defect in the left side of both retinæ, attributes his symptoms to the right eye alone. In the absence of careful investigation, therefore, the mere statement of a patient is not to be accepted as satisfactory proof that only one eye is affected. But this case is not of that nature, having been investigated by competent physicians, and is in perfect harmony with other similar cases, in which a careful perimetric exploration has shown that the eye opposite the cerebral lesion has alone appreciably suffered.

[1] A scheme suggested by Grasset (*Montpellier Médical*, 1883), in which the fibres from the outer side of both retinæ are made to decussate twice—once in the corpora quadrigemina, and again in the corpus callosum—before reaching their ultimate termination in the cortex, though it explains the possibility of monocular blindness by lesion of the internal capsule, and of hemiopia by lesion of the occipital lobe, is highly artificial, and also not in accordance with the facts of experimental lesion of the angular gyrus apart from lesion of the internal capsule.

[2] 'Case of Homonymous Hemianopia,' *Trans. Ophth. Soc.*, vol. iv. 1883.

for the partially bilateral relations of the angular gyrus. The accompanying scheme (fig. 93) more completely fulfils the various requirements, though it is to be regarded as a mere diagram, and not as an actual anatomical picture.

Each occipital lobe is in relation with the half of each retina on its own side, while each angular gyrus is in relation with the centre of the opposite eye, partly by fibres which are supposed to cross in the chiasma, and partly by fibres which reach it after decussation in the lower visual centres—possibly the corpora quadrigemina. At the same time also a partial intermingling in the chiasma of the fibres from the centre of each eye brings each angular gyrus to some extent also in

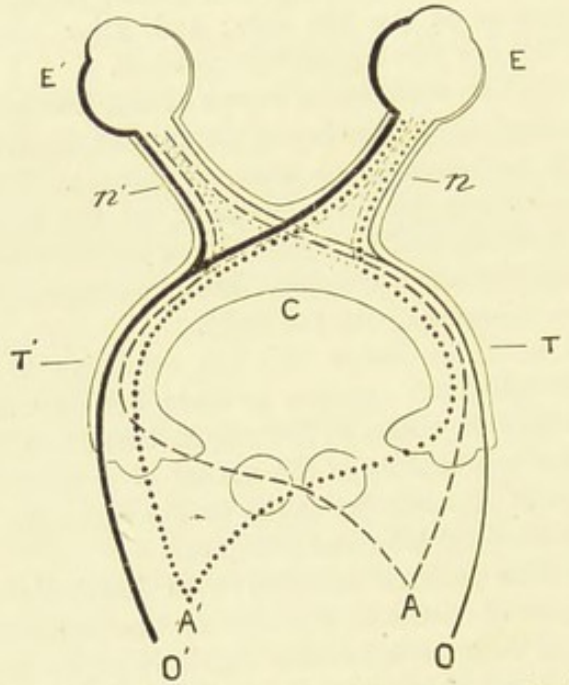


FIG. 93.—Scheme of the Optic Tracts and Visual Centres.—A, the right, and A′ the left angular gyrus. C, optic chiasma. E, the right, and E′, the left eye. *n*, the right, and *n*′, the left optic nerve. O, the right, and O′, the left occipital lobe. T, the right, and T′, the left optic tract. The thin continuous line —— represents the retinal relations of O. The thick continuous line ▬▬ represents the retinal relations of O′. The interrupted line – – – – indicates the retinal relations of A, and the dotted line . . . . the retinal relations of A′. The relations of A and A′ with the eye on the same side are indicated by finer interrupted and dotted lines respectively.

relation with the eye on the same side (see fig. 93, with description).

The relations indicated in the scheme would account for the greater affection of the opposite eye from destructive lesion of the one angular gyrus, and the bilateral amblyopia from destruction of both angular gyri. The exact extent of retinal field in relation to each angular gyrus is only a matter of

speculation; but, inasmuch as bilateral destruction of the occipital lobes in the monkey does not appreciably affect the range of vision, the angular gyri must maintain relations with the full area of clear vision, and as a matter of course specially with the maculæ luteæ. Though the destruction of one occipital lobe does not appear to cause any hemiopic defect so long as the angular gyrus is intact, yet when the angular gyrus is destroyed the removal also of the occipital lobe leads to paralysis of the corresponding side of both retinæ. In such case we should still expect to find a small area of central vision on all sides of the fixation point, innervated by the undestroyed angular gyrus of the opposite side, and the extent of the visual field will be greater on the side of lesion than on the opposite. As a matter of fact this is the condition actually demonstrated by accurate perimetric observation in a large proportion of the cases of hemiopia which have been observed in man.[1]

§ 9. But the clinical records at present existing[2] in regard to the position of the fixation point, and the condition as to central vision in cases of hemiopia, are so often marked by such laxity and imperfectness of perimetric investigation, that little reliance can be placed upon them in this relation, and the whole subject is in need of careful revision.

In a case of hemiopia, from the symptoms undoubtedly of cortical origin, reported by Sharkey,[3] there was in the eye opposite the lesion an area of normal vision extending to from 15°–55° from the fixation point, and in the eye of the same side a similar area extending from 15°–70° from the fixation point. On the other hand, Nettleship[4] has recorded a case in

[1] Wilbrand (*Hemianopsie*, Berlin, 1881) gives the proportion as thirty-three in fifty-six cases reported by various authors. Hirschberg, from his examination of cases of hemiopia, regards it as the rule that the vertical line diverges towards the defective side so as to leave an area of central vision of from 3° to 5° in extent.

[2] See on this subject Nothnagel, *Topische Diagnostik der Gehirnkrankheiten*, 1879, p. 586 *et seq.*; Bellouard, *L'Hémianopsie*, 1880; Wilbrand, *Hemianopsie*, 1881; Mauthner, *Vorträge a. d. Gesammtgeb. d. Augenheilkunde*, 1881; Starr, 'The Visual Area in the Brain, &c.' *Amer. Journ. Med. Sci.*, 1884 (a brochure, however, characterised by numerous gross inaccuracies).

[3] *Trans. Ophth. Soc.*, Oct. 1883.

[4] Nettleship, *Trans. Ophth. Soc.*, Oct. 1883.

which, from lesion of the optic tract, there was hemiopia in the eye of the same side (the other being completely blind from destruction of the optic nerve) divided exactly by a line passing through the fixation point. Other cases have been reported of hemiopia due to lesion of the optic tract, proved *post mortem*,[1] in which, though in some respects lacking in precision, the line dividing the normal and defective retinal halves appears to have been vertical through the fixation point. Inasmuch as in some cases of hemiopia it has been proved by exact perimetric investigation that the vertical line dividing the normal from the defective retinal halves has passed through the fixation point, and in others has swerved to a greater or less extent away from this point towards the defective side, and unsymmetrically in each eye, it is clear that there must be difference in causation in the two cases; and the facts and considerations which have gone before render it most probable that the differences depend on whether the optic tract itself is affected, directly or indirectly, in any part of its course as far as the primary optic nuclei, or whether the lesion is strictly cerebral. There is not on record a single case of cortical lesion limited to the occipital lobe in which hemiopia has occurred. On the other hand many cases have been reported [2] of lesion of one or both occipital lobes without any discoverable symptoms. It might be said of the cases of unilateral lesion that hemiopia may have existed and been overlooked; but this would be impossible in a case of bilateral lesion, for then the patients ought to have been blind, if lesions of the occipital lobes alone really caused hemiopia.

In most of the instances of hemiopia, which have been examined after death, in which the optic tracts, optic thalami, or corpora geniculata have not been obviously diseased, the lesions have been found in the medullary fibres of the posterior region, vaguely and inaccurately called the occipital lobe; or if the cortex has been mainly affected, the lesions have been multiple and diffuse, and not confined to the occipital region; and in addition to hemiopia there have been hemiplegia, hemianæsthesia, aphasia, or other symptoms of extensive im-

[1] See Wilbrand, *Hemianopsie*, p. 93.

[2] See the author's *Localisation of Cerebral Disease*, 1878.

plication of the cerebral tracts and centres beyond those of the occipito-angular region. It is impossible, therefore, to found on such material any accurate inductions as to the limits and relations of the visual centres. We may interpret the clinical facts in the light of experimental research, but of themselves they are altogether insufficient to establish any rigid conclusions as to the limits of the visual area, and certainly do not establish any relation between hemiopia and lesion of the occipital lobe as such, apart from the angular gyrus.

§ 10. The visual centres in the lower mammals, especially those of dogs, have been the subject of numerous investigations of recent years. Among the more important of these are the researches of Munk,[1] Luciani and Tamburini,[2] Dalton,[3] Bianchi,[4] and Loeb.[5] Those of Loeb,[6] conducted under the auspices of Goltz, are specially worthy of trust.

In none of the researches by these different experimenters, however, have the exact limits of the visual sphere in dogs been determined with any degree of accuracy or harmony. In all cases the lesions causing temporary, or enduring, disturbances of vision have involved the posterior division of the second external convolution (fig. 73, (13)); the region which, from the homology of the electrical reactions, I have indicated as the visual centre.

But none of the authors have sufficiently defined by accurate post-mortem examination the exact extent of cortex destroyed, either primarily or by secondary inflammatory processes, in

[1] *Die Functionen der Grosshirnrinde*, 1881.

[2] 'Sui Centri Psico-sensori Cerebrali' (*Rivist. Speriment.* 1879); and Luciani, in *Brain*, July 1884.

[3] 'Centres of Vision in the Cerebral Hemispheres,' *New York Med. Rec.*, 1881.

[4] 'Sulle Compensazioni Funzionali della Corteccia Cerebrale,' *Rivist. Speriment.* 1883.

[5] 'Die Sehstörungen nach Verletzung der Grosshirnrinde,' Pflüger's *Archiv*, Bd. xxxiv. 1884.

[6] This writer, however, while thoroughly exposing the falsity and absurdity of the statements of Munk, is, by reason of some strange intellectual blindness, unable to see that the very experiments on the basis of which he wages a feeble and futile polemic against cerebral localisation in reality support the truth of this doctrine in the strongest possible manner.

those cases in which the visual disorders remained permanent —the only condition which can satisfy the requirements of scientific evidence as to the true boundaries of the visual area. In some cases the disturbances of vision from unilateral lesion have been merely temporary, in others they appear to have lasted indefinitely or permanently. Until the question has been determined, how much of the cortex it is necessary to destroy in order to produce the latter effect, it is absurd to argue that because experimenters are not agreed on this point therefore there is no fixed and determinate visual area in the hemisphere. It is also premature, until this has been satisfactorily determined, to propound hypotheses as to compensation by other parts of the same hemisphere or by the other. For, so long as any portion of a centre remains, its specific function is capable of being manifested to a greater or less degree. Similarly in reference to bilateral lesions. In some cases the blindness, at first complete in both eyes, has not been permanent. But in others, as in one of Munk's experiments,[1] complete and permanent blindness in both eyes, without any other defect either as regards sensory or motor power, appears to have been produced. Such a fact shows that the recovery of vision, which others have observed even after bilateral destruction of the same region, is due merely to less complete extirpation. Differences of this kind depend in all probability on the varying extent of secondary softening in the hands of the different experimenters.

It was found by Hitzig and by Goltz that the affection of vision from unilateral lesion of the cortex manifested itself exclusively in the opposite eye. Munk[2] in his first experiments arrived at the same conclusion. Lesion at the point A (fig. 94) he found caused visual disturbances only in the opposite eye.[3]

Dalton also found that the opposite eye alone was rendered

[1] Munk, *op. cit.* p. 99.

[2] Further on this subject, and on the *presentative* and *re-presentative* relations of the cortical centres, see Chapter XII.

[3] In what is obviously merely temporary impairment of visual perception, due to only partial lesion of the visual sphere, Munk assumes the existence of what he absurdly terms 'psychical blindness' (Seelenblindheit), in contradistinction to 'cortical blindness' (Rindenblindheit).

blind, and to all appearance permanently so, when the cortex was destroyed in the region of the posterior division of the second external convolution, which he terms the angular convolution.[1]

Luciani and Tamburini, on the other hand, found that destruction of the second external convolution, more particularly of its median or parietal portion, caused blindness of the opposite eye, and also some degree of amblyopia of the eye on the same side.

§ 11. The further experiments of Munk, however, as well as those of Loeb, and also later experiments by Luciani[2] have shown that, though in dogs each visual sphere is mainly in relation with the opposite eye, it is also in relation with the outer quadrant of the eye on the same side; so that destruction of the visual centre in one hemisphere paralyses the inner three-fourths of the opposite retina, and the outer fourth of the eye on the same side. The condition, therefore—at least the enduring one—is that of homonymous hemiopia towards the opposite side, the defect in the eye opposite the lesion greatly exceeding that of the eye on the same side. But the facts recorded by Luciani and Tamburini seem to show beyond doubt that, for a short time at least, after the destruction of the middle portion of the second external convolution, there is complete blindness in the opposite eye. There is, however, no real discrepancy between these results, and we appear to have in dogs relations of the visual sphere similar to those obtaining in monkeys in the angular gyrus and occipital lobe respectively.

The middle portion of the second external convolution is

[1] Loeb makes an egregious blunder in calling the Sylvian convolution (see his figure, *op. cit.*) the angular convolution, and attributing to Dalton the localisation of the visual sphere in this region. Dalton expressly defines his angular convolution as the posterior division of the second external convolution. He describes two experiments: in the one case the lesion extended also into the convolution above and behind it, and in the other the lesion involved also the two convolutions between this and the fissure of Sylvius. The latter statement, as well as the figures illustrating the paper, should, one would think, have been sufficient to prevent such a blunder on the part of one otherwise so careful.

[2] 'Sensor. Local. in the Cortex Cerebri,' *Brain*, July 1884.

that which corresponds in its electrical reactions with the angular gyrus, and we may regard the posterior portion as the homologue of the occipital lobe.

The region which Munk defines as the visual sphere embraces a considerable extent of the posterior extremity of the hemisphere, chiefly the posterior division of the first and second external convolutions (fig. 94, A_1 A).

The point A_1, situated chiefly in the posterior division of

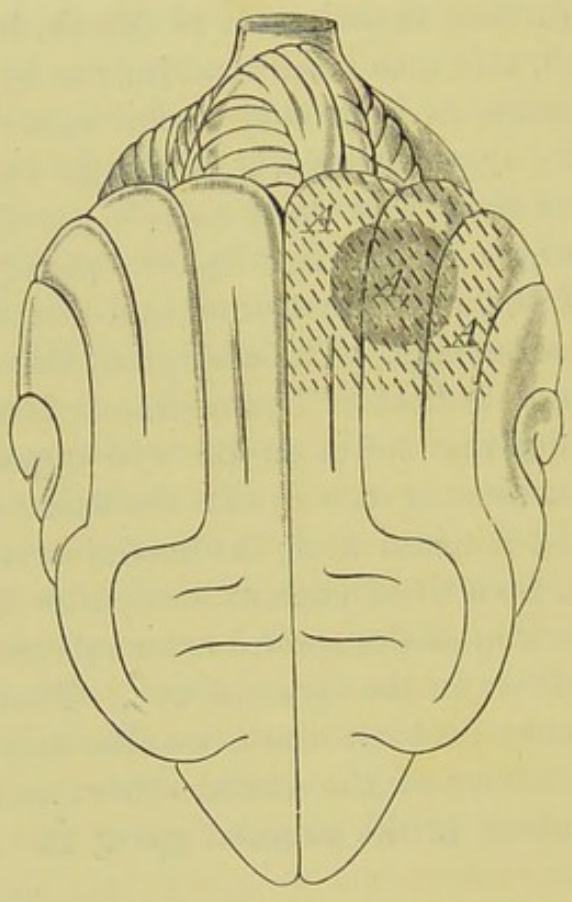


FIG. 94.—A, A_1, the Visual Area in the Brain of the Dog, according to Munk.

the second external convolution, which he first regarded as especially the depository of the visual pictures (Erinnerungsbilder) of the opposite eye, and the destruction of which caused 'psychical blindness' (Seelenblindheit)—in contradistinction to 'cortical blindness' (Rindenblindheit), to produce which it was necessary also to destroy the whole of the area marked A—he subsequently defined as the centre of clear vision in the opposite eye. Further, the mesial portion of the visual sphere, adjoining the falx, is the centre for the inner half;

the anterior portion, for the upper half; and the posterior portion, for the lower half, of the opposite retina. The lateral portion he regards as the centre for the outer quadrant of the eye on the same side.

Destruction of each portion induces blindness in the respective region of the eye on the opposite or the same side accordingly, and it is only by eccentric fixation of the eyes, or by practice, that the animal is able to overcome the defects so induced.

These statements, for which the evidence adduced by Munk appears ridiculously insufficient, have been conclusively refuted by Loeb. Loeb has shown by carefully devised experiments—in many of which he first enucleated one of the eyeballs, where it was necessary that it should be entirely eliminated—that there is no single portion of the region included within the visual zone by various authors, which may not be injured without causing any visual defect perceptible on the day after the operation. Munk's assertion that lesion of the point A_1 (fig. 94) causes defect in the point of clear vision is especially erroneous, as it is precisely this point which is least affected when visual disturbances do occur. When visual disturbances do ensue—which is the rule, and as the records of the various experiments show, particularly when secondary extension of the primary lesion occurs, or when the operations are repeated—they are invariably of the character of hemiopia or hemiamblyopia. There is no foundation whatever for the statements made by Munk that particular regions of the retina are in special relation with particular regions of the visual zone. When defect of vision occurs from lesion of the posterior lobe, it is always of the same hemiopic character, whatever region is specially injured. The lateral portion of the sphere defined by Munk is not specially in relation with the outer quadrant of the eye on the same side, nor any portion more in relation with one part of the opposite retina than another. In particular, as remarked, central vision is precisely that which is least affected in all cases, whether of unilateral or bilateral lesion of the visual zone as defined by Munk.

There is never any eccentric or abnormal fixation of the

eyeballs when the special regions indicated by Munk are destroyed, such as would necessarily result if particular portions of the retinæ were paralysed. Nor is the recovery of vision, after partial lesions of the visual zone, due to practice and the acquisition of new visual experience; inasmuch as recovery takes place when the animal is kept absolutely in the dark, and prevented from exercising its visual faculties.[1]

The results obtained by Loeb are in perfect harmony with the strict localisation of a visual sphere in the hemisphere. Partial lesions produce only transient effects, which may not be perceptible on the day after the operation. But to argue, as this physiologist does, that there is no definite visual sphere in the hemisphere because the limits may not have been correctly assigned by any of the experimenters, and because unfounded assertions have been made by Munk, is in the highest degree illogical; and he is contradicted by his own experiments, in which it is clearly shown that the degree and duration of the hemiopia varied with the degree of destruction of the occipital region, and in some cases remained permanent without any appreciable defect otherwise in the animal's powers and capacities.

On grounds of homology we have every reason for concluding that the region (fig. 73, (13)) from which electrical reactions are obtained, similar to those of the angular gyrus in monkeys, is the extreme anterior limit of the visual zone; while the posterior limits are not exactly defined, though the posterior or occipital division of the second external convolution appears to be the most important part of the visual sphere.

§ 12. The limits of the visual area in cats have not been the subject of much experimental research, but the anatomical disposition and electrical reactions of the parieto-occipital division of the second external convolution (fig. 77, (13)) indicate without doubt that this region is homologous with the visual zone of the dog's brain. That in cats also each centre is in relation with the corresponding side of both retinæ, as in dogs,

[1] That practice is of no importance, however, is not denied. The great fact is that it is not essential. 'Indess will ich nicht in Abrede stellen, dass auch die Uebung sich bei erstoperirten Thieren von Vortheil erwiesen mag' (*op. cit.* p. 60).

is more than probable. The researches of Gudden[1] and others on the constitution of the optic chiasma in cats show that, as in dogs, there is a semi-decussation of the optic tracts; and Nicati[2] found experimentally that division of the chiasma in the antero-posterior or sagittal diameter did not cause complete loss of vision in either eye; a fact explicable only on the theory of semi-decussation of the optic tracts. In one experiment which I made on a cat I observed that, after destruction of the visual zone of the left hemisphere, (fig. 77, (13)), there appeared to be complete blindness of the opposite eye, and that the animal—the left eye being closed—knocked against every obstacle in its path. On the left eye being unclosed the animal walked with greater freedom, but still occasionally knocked the side of its head. This I attributed[3] to blindness still existing in the right eye; but on again examining into the facts of the case, I am inclined to think that the true explanation was a hemiopic defect in both eyes, continuing after the temporary total blindness of the eye opposite the lesion.

As regards rodents the visual centre would, according to the homology of the electrical reactions, occupy the parieto-posterior region of the hemisphere (fig. 78, (13)), a region anatomically corresponding with (13) in the brains of the gyrencephalous animals. The exact limits of the visual zone in these animals do not appear to have as yet been experimentally determined by any inquirer, but lesion of the hemisphere of the rabbit involving the region indicated has been found by Moeli[4] to cause loss of vision in the opposite eye of a more or less temporary character.

The total loss of vision in the opposite eye observed by Moeli seems to accord with the results of sagittal section of the optic chiasma in this animal and the guinea-pig obtained by Brown-Séquard.[5] As a consequence of this operation there

[1] *Archiv f. Ophthalmologie*, Bd. xx. 1874.

[2] *Archives de Physiologie*, Ser. II. tome v. 1878.

[3] First edition, p. 170.

[4] 'Versuche an der Grosshirnrinde des Kaninchens,' Virchow's *Archiv* Bd. lxxvi. 1879.

[5] 'Sur les Communications de la Rétine avec l'Encéphale,' *Archives de Physiologie*, 1871–72.

was total blindness in both eyes. Gudden[1] also, in his first researches on this point, was of opinion that there was total decussation of optic tracts in the rabbit, and that enucleation of the eyeball, or destruction of the optic tract or centres on one side, led to complete atrophy of the opposite tract or nerve respectively. But in his later researches[2] he arrived at the conclusion that there was a small fascicle of uncrossed or direct fibres also in this animal, similar to the arrangement obtaining in the higher animals. This being the case, it would be more probable that in the rabbit also each hemisphere would have relations, to some extent at least, with the eye on the same as well as on the opposite side. Some experiments made by Munk[3] support this view, but the question is one which cannot as yet be regarded as definitively determined.

§ 13. As regards pigeons and birds generally there is a region (fig. 82, ×), electrical irritation of which causes reactions homologous with those of (13) in the brain of higher animals. The region in question occupies the parieto-posterior aspect of the hemisphere, where the cortex forms a thin lamina over the central ganglion, and corresponds anatomically with the visual zone of the gyrencephalous animals.

McKendrick[4] found that destruction of this region caused blindness in the opposite eye; whereas removal of the anterior part of the hemisphere had no effect on vision, nor removal of the posterior extremity of the hemisphere. Similar results have been obtained by Jastrowitz.[5]

Blaschko,[6] however, found that vision did not seem entirely abolished in the opposite eye by destruction of the cortex in the region indicated; and Munk,[7] continuing his researches, came to the conclusion that, though vision seems at first to be entirely abolished in the opposite eye, yet after a time it

[1] *Archiv f. Ophthalmologie*, Bd. xx. 1874.

[2] *Ibid.* Bd. xxv. 1879.

[3] *Ueber die centralen Organe für das Sehen u. d. Horen bei den Wirbelthieren*, 1883.

[4] 'Observations and Experiments on the Corpora Striata and Cerebral Hemispheres of Pigeons,' *Trans. Roy. Soc. of Edinburgh*, January 1873.

[5] *Archiv für Psychiatrie*, Bd. vi. 1876.

[6] *Inaugural Dissertation*, Berlin, 1880.

[7] *Memoir cit. sup.*

appears that the extreme outer or lateral region of the retina is not paralysed; indicating that each hemisphere, as in the higher animals, is partially in relation with both eyes.

It is usually stated that in pigeons a complete decussation of the optic tracts occurs in the chiasma; but Gudden,[1] who at first regarded this as beyond all doubt, questions whether there may not be some uncrossed fibres in these animals as well as in rabbits.

That even in the pigeon, with its widely separated and laterally placed eyes, a certain amount of binocular vision is possible was indicated by Müller,[2] who found, in addition to the usual *fovea centralis*, another fovea, situated nearer the temporal region of the retina. The outer foveæ would serve for binocular, and the central foveæ for monocular vision.

Müller's statements as to the existence of two foveæ have been confirmed by Hirschberg[3] by ophthalmoscopic examination. These observations have been quoted by Munk in corroboration of his experimental results, to which, if correct, they undoubtedly lend considerable support.

§ 14. That the visual area of the cortex is not merely a functionally differentiated region capable of being replaced by some other portion of the hemisphere, but anatomically the central expansion of the optic radiations, and therefore structurally distinct from all other centres, is proved by the atrophy which ensues in the primary optic centres, tracts, and nerves when the visual zone proper is destroyed, and by the atrophy occurring in, and strictly confined to, the region included within the visual zone when the optic radiations are severed.

That atrophy occurs in the primary centres, tracts, and nerves from lesion of the visual zone of the cortex, altogether apart from direct injury to these structures, has been abundantly proved. In one of the experiments above related, in which the animal was rendered completely and permanently blind, the gradual evolution of atrophy of the optic discs was distinctly traced during life; and after death the optic nerves, tracts, and primary centres were found to be greatly reduced

[1] *Archiv für Ophthalmologie*, Bd. xxv. 1879.

[2] Heinrich Müller, *Gesammelte Schriften* (by Becker), 1872, p. 143.

[3] 'Zur vergleichende Ophthalmoscopie,' Du Bois-Reymond's *Archiv*, 1882.

in size as compared with those of a normal brain. Similar facts have been recorded in connection with lesions or defects in the occipito-angular region in man.[1]

Gudden[2] found that destruction of the cortex in the left parieto-occipital region in a new-born puppy led to atrophy of the left corpus geniculatum externum, left anterior tubercle of the corpora quadrigemina, the left optic tract, and to some extent of the right optic nerve.

Monakow[3] observed similar results in rabbits on destruction of the occipital region; and Ganser[4] the same in cats on destruction of the cortex, involving the parieto-occipital region. Monakow has further shown that the atrophic changes, consecutive to destruction of the cortical visual centres, affect special tracts and structures, viz. the optic radiations, median medullary layer (fig. 49, *m m*) of anterior tubercle, and the cells of the corpus geniculatum externum and pulvinar; whereas when the eyeball is enucleated the atrophic changes occur in the gelatinous ground-substance of the corpus geniculatum externum, pulvinar, and anterior tubercle of the corpora quadrigemina, and in the last also in the cells of the superficial grey layer.

It thus appears that of the structures composing the primary optic nuclei some are more immediately related to the cortical centres, others to the optic tracts; and that between these two connections exist, which serve to establish an indirect relationship between the eyes and the cortical visual sphere. But while destruction of the cortical centres leads indirectly to atrophy of the optic tracts, it has not been satisfactorily established that enucleation of the eyeball leads to atrophy extending beyond the primary centres. Neither Gudden, nor Ganser, nor Monakow has been able to discover any indubitable cortical atrophy after enucleation of the eyeball in cats, dogs, or rabbits. Hence, though such an occurrence

[1] See Sharkey's case, already referred to, p. 290. Monakow (*Archiv f. Psychiatrie*, Bd. xiv. 1883) has minutely investigated a similar case of atrophy of the optic tracts in connection with porencephalic defect of the occipito-angular regions. Dr. Cobbold, of Earlswood, has submitted to me for examination the brain of an idiot in which the same condition existed.

[2] *Archiv f. Ophthalmologie*, Bd. xxi. 1875.

[3] *Archiv f. Psychiatrie*, Bd. xii. 1881.

[4] *Ibid.* Bd. xiii. 1882.

is theoretically possible, especially in cases of congenital absence of the organ of vision, or removal before it can have been employed to any extent as a channel of perception, the statements of some authors that they have observed secondary atrophy of the visual zone consecutive to the enucleation of the eye or eyes, must be viewed with considerable caution. The atrophic changes seem to be arrested in the primary centres. But when the optic radiations themselves are severed, as in certain experiments on rabbits made by Monakow, atrophy extends both centrally and peripherically.

In the latter case the atrophic changes are exactly such as result from destruction of the cortical visual area itself. In the former the atrophy becomes manifest in the region embraced in the visual zone (parieto-occipital region), and particularly affects the third and fifth layers of the cortex—viz. the layer of granules and large pyramidal cells, and the layer of multipolar cells immediately external to the medullary layer, which is also remarkably reduced.

Monakow therefore concludes that the optic radiations are specially connected with the third and fifth layers of the cortex in the visual area. A further confirmation of these interesting and important observations is eminently desirable.

But it follows from the various facts recorded that the localisation of a special area of visual perception in the cortex is based on structural as well as functional relations with the eyes; so that a functional equivalence or indifferentism of the various regions of the cortex and the theory of one region compensating for the loss of another are assumptions which involve anatomical impossibilities.

Part II.—*The Auditory Centre.*

§ 15. Among the reactions consequent on electrical irritation of the hemisphere there is one the significance of which might almost be deduced *a priori*. The reaction in question is that which occurs on electrical irritation of the superior temporo-sphenoidal convolution, viz. pricking of the opposite ear, associated with wide opening of the eyes, dilatation of the pupils, and turning the head and eyes to the opposite side.

These phenomena are just such as occur when a loud sound is made in immediate proximity to the opposite ear. Taking a monkey I placed it on a table, and while all was still I made a shrill whistle close to the animal's right ear. Immediately the ear was pricked, and the animal turned with a look of intense surprise, with eyes widely opened and pupils dilated, to the direction from which the sound proceeded. On repetition of the experiment several times, though the pricking of the ear and turning of the head and eyes in the direction of the sound invariably occurred, the look of surprise and dilatation of the pupils ceased to be manifested. From the mere character of the reactions, therefore, it might be fairly concluded that irritation of the superior temporo-sphenoidal convolution arouses subjective auditory sensations, of which the pricking of the ear, and attitude of surprise, or excited attention, are merely the outward physical manifestation.

Equally, if not more characteristic, are the effects observed on stimulation of the homologous region in the brains of the lower animals, whose habits are such as to make their safety largely dependent on the acuteness of their hearing. In the cat, dog, and jackal this region is embraced in the posterior division of the third external or supra-Sylvian convolution (figs. 73, 75, 77, (14)). In all these pricking of the opposite ear was invariably seen, but the rest of the associated reactions varied in intensity.

In the brain of the rabbit stimulation of the corresponding region (fig. 78, (14)) caused also pricking of the opposite ear, frequently associated with turning the head and eyes in the supposed direction of the sound. But in the wild jackal and timid rabbit there was not only the reflex pricking of the ear, but the quick start or bound, as if to escape from danger, such as might be indicated by loud or unusual sounds. In the pigeon the absence of the auricle renders it more difficult to fix on any simple movement as the associated expression of auditory sensation, but in this animal also the occasional turning of the head to the opposite side, on stimulation of the parietal region below and behind the visual centre, is in all probability of the same nature as the foregoing.

But in addition to the strong presumption furnished by the character of the electrical reactions that the superior temporo-sphenoidal convolution in the monkey (or its homologues in the brain of the lower animals) is the centre of hearing, the results of localised destruction of this convolution are such as to prove this beyond all doubt.

To test the sense of hearing in the lower animals, and to distinguish between mere reflex reaction to auditory impressions and auditory sensation proper, is a matter of some difficulty; and it is especially difficult to determine the existence of unilateral deafness, on account of the impossibility of absolutely restricting sonorous vibrations of any intensity to one side alone. By plugging the one ear this may in a measure be overcome, if the test sounds are not of great intensity; but the possibility of conveyance of sonorous vibrations through the skull, apart from the tympanic apparatus, must always be taken into account.

§ 16. In several preliminary experiments[1] on the temporo-sphenoidal lobe the lesion was not confined to the superior temporo-sphenoidal convolution, but when this was involved on the one side there was absence of the usual reaction to auditory stimuli proper when the ear of the same side was securely plugged. When the lesion was bilateral there was total absence of response to auditory stimuli, which usually excite active reaction and signs of attention.

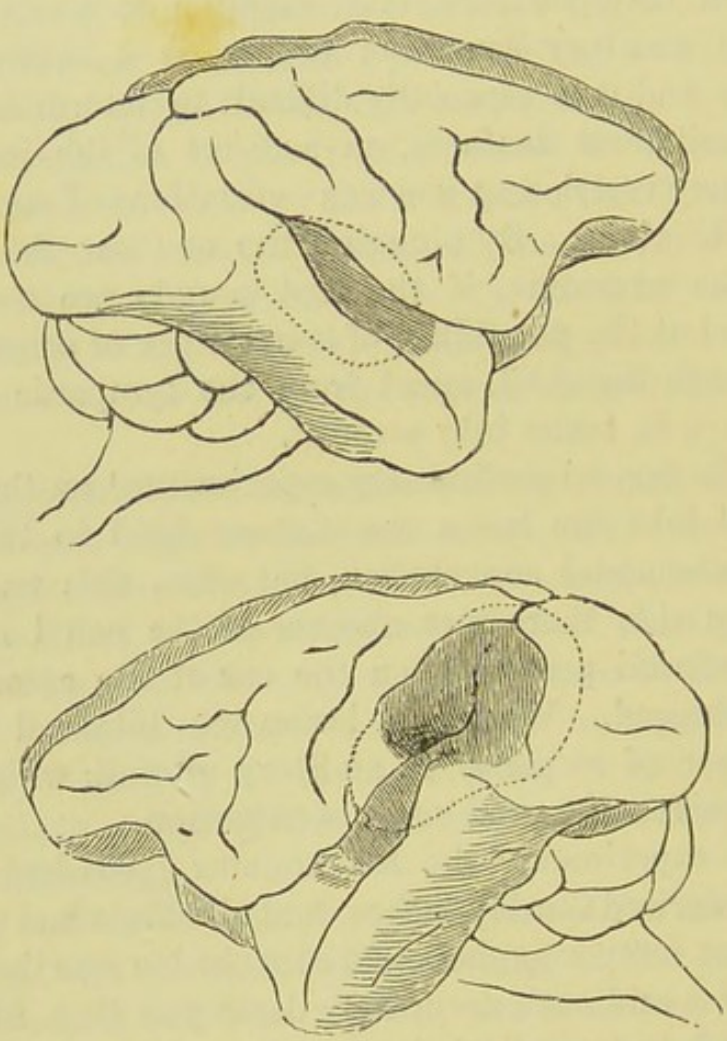
In one experiment[2] the left angular gyrus had been previously cauterised the day before, and all effects had passed off. The superior temporo-sphenoidal convolution was then exposed on both sides and each accurately destroyed (figs. 95, 96).

Repeated tests indicated retention of tactile sensibility, taste, smell, and vision, and complete volitional motor power. But hearing was to all appearance entirely abolished. As the animal was keenly on the alert, it was not easy to devise an entirely satisfactory test without arousing its attention otherwise. In order to avoid attracting its attention by sight, I retired into another room, and watched the animal through

[1] Experiments XI., XII., XIII., XIV., *Phil. Trans.* vol. clxv., Part II.

[2] Exp. XV., *ibid.*

a chink in the door. While it sat comfortably before the fire it paid no attention whatever to loud calls, shrill sounds, or whistling. For purposes of comparison another monkey, whose powers of hearing were undoubted, was placed with it as a companion, and the tests repeated as before. The difference in the behaviour of the two was most striking. While the normal monkey became startled at each sound, and peered

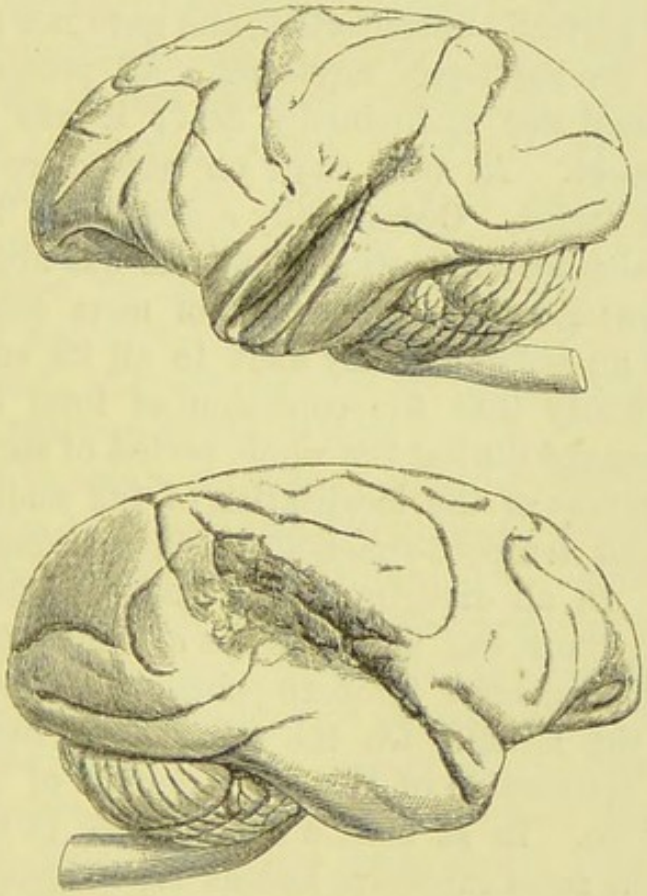


FIGS. 95 and 96.—The shading in these figures indicates the position of the lesions of the cortex in the hemispheres of the monkey, causing loss of hearing in both ears and temporary loss of sight in the right eye. The dotted line indicates the extent of the surface exposed by removal of the skull. (Roy. Soc.)

about curiously to ascertain its origin, the other appeared altogether unconcerned. By repeated and otherwise varied tests it was clearly established that the animal was perfectly indifferent to sounds which in other monkeys excite lively reaction, while in all other respects it was quick and keenly responsive. Beyond this, as a proof of deafness, it seems impossible to go in the lower animals. The same result is

further conclusively demonstrated in the following experiment, in which also the permanency of the symptoms is satisfactorily shown.

In this animal[1] the superior temporo-sphenoidal convolution was cauterised in both hemispheres; and, as was found on careful examination,[2] the lesions were accurately confined to this convolution in both hemispheres, without inflammation or secondary extension. The animal was allowed to survive



FIGS. 97 and 98.—Destruction of Superior Temporo-sphenoidal Convolution on both sides, causing complete deafness. (From photographs.)

for more than a year, during which time, from the beginning till the end, it enjoyed perfect health and the full enjoyment of all its faculties and powers, with the single exception of hearing. No sign of hearing, or even twitching of the ears, could be elicited by sounds which invariably attracted the

[1] Experiment 13*, *Phil. Trans.* Part II. 1884.

[2] See the series of photographs of sections illustrating the text, Plate 22 (figs. 23-38).

attention of other monkeys which were its companions, or which were subjected to the same conditions.

Six weeks after the operation the animal was exhibited before the physiological section of the International Medical Congress in London, 1881,[1] along with another monkey affected with right hemiplegia from lesion of the motor area of the left hemisphere. While it was climbing about, and disporting itself before the audience, a percussion cap was exploded, causing the hemiplegic monkey to start suddenly, while this one remained perfectly unconcerned, and gave not the slightest indication of having heard anything. All present admitted that the animal was undoubtedly deaf; it was defective in no other respect. As time went on tests were continually repeated and varied. Occasionally a doubt was raised as to whether the absence of reaction to sounds was absolute. But careful examination, and elimination of mere coincidences of movement in an animal keenly alert to all its surroundings, established clearly that the condition of total deafness remained unchanged during the whole period of survival.

Further proofs of the localisation of the auditory centres in the superior temporo-sphenoidal convolutions are almost superfluous. In all experiments on the temporo-sphenoidal lobe in which there was any evidence of impairment or loss of hearing, the superior temporo-sphenoidal convolution was involved in the lesion. On the other hand hearing is not impaired by destruction of any other portion of the temporo-sphenoidal lobe. In at least a dozen cases in which I have established the most extensive lesions in, or entirely removed the whole of, the temporo-sphenoidal lobe, with the exception of the superior temporo-sphenoidal convolution, on one or both sides, I have obtained clear indications of the continuance of signs of perception of auditory stimuli, indicated by twitching of the ear and turning to the origin of slight sounds, such as tapping, scratching, or whispering close to the ear. My results have been entirely confirmed by Horsley and Schäfer, who have informed me that their experiments have shown that it is only when the superior temporo-sphenoidal

[1] See *Transactions of the International Medical Congress*, 1881, vol. i. p. 237.

convolution is destroyed that hearing is impaired or abolished, and that no such effect is produced by entire removal of the rest of the temporo-sphenoidal lobe.

§ 17. As to the position of the auditory centre in dogs and the other lower mammals we should, even without further experimental demonstration, have good reason for localising it in the region which reacts similarly to that of the monkey on electrical excitation (see area (14), figs. 73, 75, 77, 78).

Munk states [1] that a destructive lesion in both hemispheres, established primarily towards the lower extremity of the third external convolution, and involving also the adjacent extremity of the second external convolution, causes temporary impairment of hearing, which, as in the case of vision, he calls 'psychical deafness.' This, however, in the course of a few weeks entirely disappears, so that at the end of this time no difference from the normal can be detected. At first, however, before the disturbances induced by the primary lesion have subsided, the animal appears to be totally deaf, and exhibits no reaction to the loudest sounds.

In order to secure total and enduring deafness—absurdly termed by him 'cortical' (Rindentaubheit) in contradistinction to 'psychical' deafness (Seelentaubheit)—Munk states that destruction not merely of the posterior division of the third external convolution, but also of the posterior divisions of the first and second convolutions, is necessary. His experiments on this point are, however, exceedingly unsatisfactory; and that his conclusions are erroneous has been demonstrated by Luciani and Tamburini [2] who have found that bilateral destruction of the posterior division of the third external convolution alone produces total deafness; while destruction of the posterior division of the second external convolutions has no effect on the sense of hearing whatever. Munk's primary lesion destroys only a portion of the true auditory centre, and the secondary disturbances which are set up by the lesion functionally annihilate the whole for the time being. For the time, therefore, the animal appears wholly deaf But when the secondary disturbances have subsided, the uninjured

[1] *Op. cit.* p. 40.

[2] *Sui Centri Psico-sensori Corticali*, 1879.

portion of the auditory centre is able to resume its functions, and the animal recovers its hearing.

In order that deafness should be permanent the whole of the posterior division of the third external convolutions must be destroyed, and it is not necessary that the lesion should extend beyond these.

Though similar experiments have not as yet been carried out on other mammals, we have every reason to believe that destruction of the regions homologous in their electrical reactions will yield results as regards the sense of hearing entirely in accordance with those obtained in monkeys and dogs. From these it is apparent that the posterior division of the Sylvian convolution in the dog is not the homologue of the first or superior temporo-sphenoidal convolution in the monkey, as has been assumed by Meynert.[1] The homology lies between the superior temporo-sphenoidal and the posterior division of the supra-Sylvian or third external convolution.

Though anatomically the posterior division of the Sylvian convolution appears to correspond with the superior temporo-sphenoidal, the resemblance is only superficial, and is conditioned by the shallowness of the fissure of Sylvius in the dog, as compared with that of the monkey. In all probability the Sylvian convolution of the dog is represented within the lips of the fissure of Sylvius in the brain of the monkey, overlapping and concealing the deeply seated insular lobule, or island of Reil.

Part III.—*The Olfactory and Gustatory Centres.*

§ 18. The position of the olfactory centre may with great probability be inferred from anatomical considerations alone, apart from actual experiment.

We have already seen (Chapter I. § 21) that the olfactory bulb and tract are the modified remnants of a hernia-like protrusion of the cerebral vesicle anteriorly, such as permanently characterises the rhinencephalon of the frog.

[1] 'Die Windungen der convexen Oberfläche des Vorder Hirns,' *Archiv f. Psychiatrie*, Bd. vii. 1877.

The anterior portion of the protrusion becomes the olfactory bulb, while the rest of the walls coalesce to form the olfactory tract, the original cavity becoming obliterated, so that only traces remain. The roots of the tract, or remnants of the lateral walls of the rhinencephalon, diverging from the point where the original cavity becomes shut off from the anterior cornu (*trigonum olfactorium*), are continuous respectively with the anterior and posterior or lower extremities of the great limbic or falciform lobe, which, bent round the corpus callosum, constitutes the internal margin of the hemisphere. Broca[1] aptly compares the connections of the olfactory bulb and tract with the falciform lobe to a tennis racquet, of which the olfactory tract forms the handle, and the falciform lobe the circumference. The inner root fuses with the anterior extremity of the gyrus fornicatus or callosal convolution, while the outer root fuses with the anterior extremity of the hippocampal convolution or hippocampal lobule (uncus, subiculum, pyriform lobule, &c.)

The region of the trigonum olfactorium is considered by Broca to constitute a third root (the grey root), containing fibres which connect the tract with the cortex at the base of the orbital convolutions (the anterior olfactory centre).

According to the degree of development of the sense of smell in different animals, the structures above described, or certain portions of them, vary enormously; so that Broca divides all animals into '*osmatics*' (including the great majority of mammals) and '*anosmatics*,' in which the sense of smell is relatively feebly developed (primates, amphibious carnivora); rudimentary (balænidæ); or altogether wanting (delphinidæ).

In the osmatics (cat, dog, rabbit, &c.) the olfactory bulbs and tracts are very large, and the hippocampal lobule in particular of all other cerebral regions attains remarkable proportions, so that in these animals it forms a distinct protuberance in the lower temporo-sphenoidal region (fig. 73). In the anosmatics, on the other hand, the hippocampal lobule is small, though distinct, in those—such as the monkey and

[1] *Revue d'Anthropologie*, 1878; *Anat. Comp. des Circonvolutions Cérébrales*; *Recherches sur les Centres Olfactifs*; *Ibid.* 1879.

man—in which smell is good, but secondary to other sensory faculties; while in the balænidæ [1] it is greatly reduced, and in the dolphin quite rudimentary. Though there appears also to be a relation in the osmatics between the size of the internal root and the anterior portion of the callosal convolution—where Broca supposes a superior olfactory centre to exist—yet that there is no real concomitance between the two is shown conclusively by the brain of the cetaceans, in which,

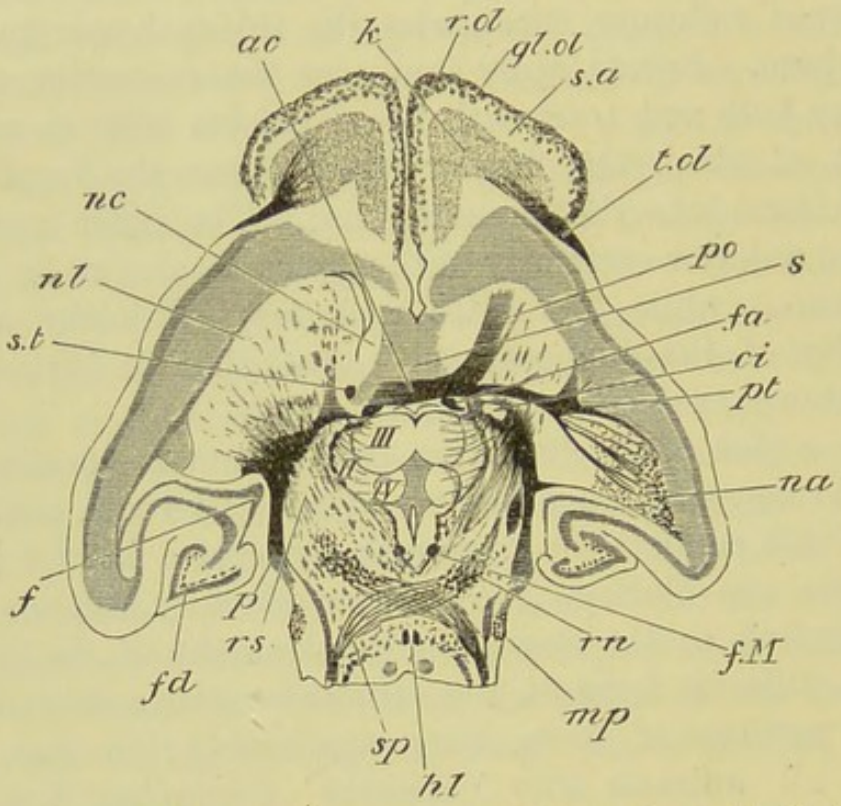


FIG. 99.—Horizontal Section of the Brain of the Mole on a level with the anterior commissure (× 4). (After Ganser.)—*ac*, anterior commissure, dividing into *po*, pars olfactoria, and *pt*, pars temporalis. *ci*, internal capsule. *f*, fimbria. *fa*, anterior pillar of fornix. *fd*, fascia dentata. *f*M, Meynert's fasciculus. *gl.ol*, glomeruli olfactorii. *hl*, posterior longitudinal fasciculus. *k*, granular layer of olfactory bulb. *mp*, middle peduncle of cerebellum. *na*, nucleus amygdalæ. *nc*, nucleus caudatus. *nl*, nucleus lenticularis. P, pyramidal tract. *rn*, red nucleus. *r.ol*, roots of the olfactory nerve. *rs*, regio subthalamica. *s*, septum lucidum. *sa*, substantia alba. *sp*, superior cerebellar peduncles. *st*, stria terminalis. *t.ol*, tractus olfactorius.

though the sense of smell is rudimentary or absent, the anterior portion of the callosal convolution is specially well developed; a fact which Broca himself admits to be apparently in flagrant contradiction to his hypothesis. Not only is the callosal convolution large, but it is moreover much

[1] 'Sur l'Encéphale des Balænidæ,' by Beauregard, *Journ. de l'Anat. et de la Physiologie*, tome xix. 1883.

more richly convoluted than is the case in the great majority of mammals. Hence it is obvious that we cannot regard the relationship which Broca would seek to establish between the internal or superior olfactory root and the callosal convolution as at all justified on anatomical grounds.

The only relationship which undoubtedly exists is between the size of the olfactory bulb and the hippocampal lobule or anterior third of the hippocampal convolution. That the rest of the falciform lobe is related to other functions than the sense of smell is a conclusion clearly indicated by comparative anatomy, and demonstrable, as will be shown subsequently, by physiological experiment (§ 25).

§ 19. The anatomy and connections of the anterior commissure (fig. 99, *a c*) are further of great significance as to the position of the olfactory centres. This commissure, as has been described above (Chapter I. § 18), consists of two divisions, an anterior and posterior. The anterior division is the commissure between the olfactory bulbs, and varies in size with these. The posterior division is traceable outwards to the region of the hippocampal lobule and nucleus amygdalæ (Luy's ganglion olfactif), and is obviously a commissure of centres related to the olfactory organs.

Ganser,[1] however, has pointed out that the size of the posterior or temporal division does not vary simply with the size of the pyriform lobule. Thus in the dog, whose pyriform lobule is seven times as large as that of the rabbit, the temporal division of the anterior commissure is a third smaller. What may be the significance of this fact is not quite clear, though it is probably an index of the degree of association of the two centres with each other. *Cæteris paribus*, the smaller the temporal division, the greater the independence of the respective centre in each hemisphere.

§ 20. Passing next the results of electrical irritation of the hippocampal lobule, we obtain very significant indications of subjective olfactory sensation.

As above described (Chapter VIII.) irritation of this region in the monkey, cat, dog, and rabbit was attended by

[1] 'Ueber die vordere Hirncommissur der Säugethiere,' *Archiv für Psychiatrie*, Bd. ix. 1879.

essentially the same reaction in all, viz. a peculiar torsion of the lip and nostril on the same side. This reaction is precisely the same as is induced in these animals by the direct application of some strong or disagreeable odour to the nostril, and is evidently the outward, or associated, expression of excited olfactory sensation. The reaction in this case is on the same side as the irritation, and is thus unlike all the other reactions which ensue on irritation of the hemisphere elsewhere.

Only occasionally was the reaction bilateral, except in the rabbit, where this occurred as the rule.

The direct or uncrossed reaction of the hippocampal lobule is what we should naturally expect from the anatomical disposition of the olfactory tracts. Each olfactory tract is connected only with the hemisphere on the same side—the inner root with the anterior or superior extremity of the falciform lobe, the outer with the posterior or inferior extremity of the same. Though, as has been mentioned, Broca was of opinion that the connection of the inner or superior root indicated the existence of an olfactory centre in the anterior part of the callosal convolution, yet the brain of the cetaceæ does not support this view; and it is more probable that the inner root is, in reality, connected by the longitudinal fibres of the callosal convolution with the hippocampal lobule. Two separate olfactory centres in one hemisphere, to say nothing of a third centre, which Broca also supposes to exist at the base of the orbital convolutions, cannot be regarded as probable or justified by mere anatomical appearances alone.

But in any case all the connections of the olfactory tract are with the hemisphere of the same side. Meynert assumes the existence of a decussation of the olfactory tracts in the anterior commissure; but the investigations of Gudden and Ganser are entirely opposed to this hypothesis. Anatomically there are no appearances of decussation of the olfactory and temporal divisions of the anterior commissure; and when one olfactory bulb is removed, the whole of the olfactory division disappears on both sides; while the temporal division remains intact and unchanged. These results are altogether opposed to the theory of decussation, and we may regard it as established that the anterior commissure is not an olfactory

chiasma in the same sense as the optic commissure. There is therefore no anatomical basis of connection between the olfactory tract and the opposite cerebral hemisphere.

§ 21. There is considerable difficulty in determining the effects of destructive lesions of the hippocampal lobule. Apart from the difficulties of testing the sensibility to odours proper in the lower animals, as distinguished from mere irritants of the Schneiderian membrane, it is practically impossible to establish lesions in the hippocampal lobule without injury to neighbouring regions. Hence the accurate determination of the centre of smell by destructive lesions involves considerable complications. But by processes of exclusion, and by the various considerations above mentioned, the localisation of the olfactory centre seems capable of being arrived at with a considerable degree of precision.

In the first experiment [1] made in reference to this question the left temporo-sphenoidal lobe was deeply divided transversely in a line coinciding with the anterior prolongation of the inferior occipital sulcus, and the greater portion of the superior, middle, and inferior temporo-sphenoidal convolutions disorganised and scooped out. The lower extremity of these convolutions remained uninjured superficially, though almost entirely severed from their connections above. The hippocampal convolution, however, was not severed.

As the result of this lesion it was observed that hearing was diminished, or abolished, on the right side, in relation with the lesion of the superior temporo-sphenoidal convolution. Owing to the difficulty of preventing diffusion to both sides of the mouth, no accurate determination could be made as to the sense of taste, though there appeared to be less sensitiveness to acid on the right side of the tongue. The vapour of acetic acid, however, caused distinctly less reaction in the left nostril than in the right. In this case also some defect of tactile sensibility was observed on the right side.

There was thus a complex assemblage of phenomena, some of which—the deafness on the right side—are explicable by previous experiments, while others—the defect of tactile sensibility on the right side—will be further elucidated below

[1] Experiment XI., fig. 13, *Phil. Trans.* vol. clxv. Part II. 1875.

(§ 25). The symptoms also indicated that the centres of smell on the same side, and taste on the opposite, were involved in the lesion.

In a second experiment[1] a similar lesion was established in the left hemisphere, but passing more deeply into the hippocampal region, and more completely severing the lower portion of the temporo-sphenoidal lobe from the rest.

Hearing was impaired or abolished on the right side, the superior temporo-sphenoidal convolution being destroyed. Sight was unaffected. Tactile sensibility was at first impaired, and ultimately on the third day almost completely abolished on the right side. Smell appeared defective or lost on the left side, as judged by the following facts. The animal took a piece of apple offered it, and after smelling it began to eat. The right nostril was then stopped up, and when a piece of apple was again offered the animal seized it, and held it to its nostrils repeatedly, as if it had difficulty in making out the nature of the object by its sense of smell.

In a third experiment[2] both temporo-sphenoidal lobes were broken up and disorganised—on the left side more completely than on the right.

Sight was unimpaired, but hearing was entirely abolished on both sides, no response being elicited by the loudest sounds. Tactile sensibility was at first somewhat defective on the right side, and next day, as the process of softening advanced, very considerably diminished on this side.

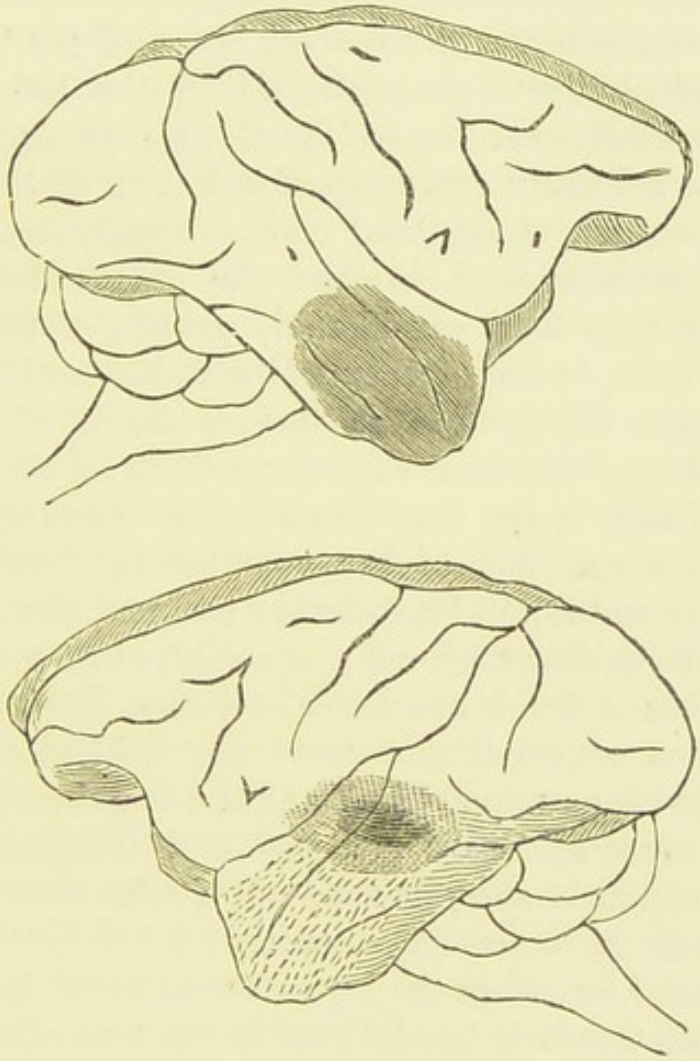
Acetic acid caused no reaction when held before the nostrils or placed in the mouth. Only when the acid was placed within the nostrils did any reaction occur; an effect evidently due to irritation of the nerves of common sensation in the nostrils, and more marked on the left than on the right side, on which there was some defect of tactile sensibility.

In this case, therefore, in which the lower portion of the temporo-sphenoidal lobes was disorganised smell and taste seemed abolished.

In a fourth experiment[3] the lower extremity of the

[1] Experiment XII., figs. 14 and 15, *op. cit.*
[2] Experiment XIII., figs. 16 and 17, *op. cit.*
[3] Experiment XIV., figs. 18 and 19, *op. cit.*

temporo-sphenoidal lobe was thoroughly disorganised on both sides, the lesion on the left side destroying also the hippocampal region very extensively. As the result of this bilateral lesion, tactile sensibility was abolished on the right side. Neither aloes nor colocynth, nor citric acid, which in ordinary conditions excite lively indications of sensation, caused the



FIGS. 100 and 101.—Lesions of the Right and Left Hemisphere, causing loss of taste and smell. (Roy. Soc.) In the right hemisphere (100) the shading indicates the extent of destruction of the grey matter. In the left (101) the dark shading indicates the superficial extent of the wound; and the dotted lines the extent of internal destruction of the lower portion of the temporo-sphenoidal lobe.

slightest reaction when placed on the tongue. The vapour of acetic acid held close to the nostrils caused no reaction. When it was introduced within the nostrils, a remarkable difference was observed between the reactions of the right and left respectively. On the right side, which was also devoid of common sensibility, acetic acid caused no reaction whatever.

On the left side copious lacrymation ensued—from the left eye particularly. Not merely was there entire insensibility to sapid stimuli on the tongue, but there appeared also an abolition of common sensibility; so that the tongue could be pricked or touched with a heated wire without exciting any motor reaction.

The facts of this experiment indicate abolition of smell, taste, and tactile sensibility on both sides of the tongue, and of tactile sensibility on the right side of the body. The reaction of the left nostril to acetic acid, viz. the copious lacrymation, was evidently due to mere irritation of the nerves of common sensation of the nasal mucous membrane.

As has been already observed, the lesions described, implicating as they do a considerable portion of the temporo-sphenoidal lobe, do not of themselves indicate with precision the respective centres of the various forms of sensibility, general and special, which were observed to be affected. But we have already seen that affections of hearing are to be ascribed to destruction of the superior temporo-sphenoidal convolution; and it will be shown in the next section that the affections of tactile or common sensibility are to be referred to destruction of the hippocampal region. Excluding these, the affections of smell and taste are evidently related to lesions of the hippocampal lobule and the neighbouring regions. The facts of comparative anatomy and the phenomena of electrical irritation show beyond all doubt that the hippocampal lobule is the centre specially related to the sense of smell. Munk[1] considers the hippocampal gyrus as the centre of smell from the facts he observed in the case of a dog which had been rendered blind by bilateral lesion of its occipital regions. This animal seemed to be unable, like other dogs, to detect by smell pieces of meat laid before it. After death it was found that the hippocampal gyri had been secondarily almost entirely converted into cysts distended with fluid. Though Munk adduces this case to show that the hippocampal gyri are the centres of smell, yet, inasmuch as the hippocampal lobules were implicated in the lesion, the case is evidently as merely another confirmation of the facts above

[1] *Die Functionen der Grosshirnrinde*, p. 130.

related in favour of the localisation of the olfactory centres in the hippocampal lobules proper.

§ 22. As to the sense of taste I have not succeeded in differentiating any special region related to this faculty, but that it is in close relation with the olfactory centre is probable from the facts described. It was noted in connection with electrical irritation of the lower extremity of the temporo-sphenoidal convolutions in the monkey, and of the same region in the brain of the cat, that movements of the lips, tongue, cheek-pouches, and jaws were occasionally induced—phenomena which might be regarded as indications of the excitation of gustatory sensation. This interpretation receives support from the above-described results of destructive lesions; and we have, therefore, reasonable grounds for concluding that the gustatory centres are situated at the lower extremity of the temporo-sphenoidal lobes, in close relation with those of smell. This would enable us to explain the occasional occurrence in man of anosmia and ageusia as the result of severe blows on the head, especially the vertex. A blow in this region causes counterstroke of the base of the brain, particularly in the region of the olfactory centres. No doubt many of the cases of so-called loss of taste and smell are merely cases of loss of smell only, the impairment of taste extending only to the perception of flavours, which, as is well known, are compounded of taste and smell together. But there are cases in which both smell and taste proper are impaired or abolished by cranial injuries,[1] and it is permissible to suppose that this may be caused by concussion and contusion of the lower extremities of the temporo-sphenoidal lobes, where the olfactory centres certainly, and the gustatory centres in all probability, are situated.

Both anatomy and experimental physiology show that the olfactory centre is situated on the same side as the corresponding peripheral organ—unlike the other sensory centres of the cerebral hemisphere.

Cases have been reported by W. Ogle,[2] Fletcher and

[1] See *Localisation of Cerebral Disease*, 1878, p. 138.

[2] 'Anosmia,' *Med.-Chir. Trans.* 1870, Cases 8, 9, and another mentioned in to note p. 275.

Ransome,[1] of the occurrence of loss of smell in the left nostril, with right hemiplegia and aphasia. Though the exact locality of the lesion in such cases may not be considered as satisfactorily established, yet, as the symptoms were such as are known to be associated with embolism of the middle cerebral artery, we have reason to regard the anosmia as in all probability due to softening of the region of the hippocampal lobule.

But there are certain facts in human pathology which would seem at variance with these results. In the condition termed cerebral hemianæsthesia—hysterical or alcoholic—smell appears to be impaired or lost on the same side as the other faculties of sense, general and special. Different interpretations have been given of the pathology of hysterical hemianæsthesia; but, assuming that it depends on some affection of the opposite cerebral hemisphere, the apparent loss of smell is explicable by the anæsthetic condition of the nostril. Magendie[2] found that smell was abolished by section of the fifth nerve. This experiment seemed to show that the integrity of the common sensory nerve of the nostril was a necessary condition of smell proper. In a case reported by Magnan, smell progressively failed with the impairment of common sensibility in the nostril, and disappeared *pari passu* with it. Even, however, when common sensibility was entirely gone in the nostril, the vapour of acetic acid caused copious lacrymation; a fact which showed that certain afferent nerves remained functionally active—presumably the olfactory—which, however, owing to loss of common sensibility, were not of themselves sufficient to convey the impression of odours. In the monkey, above referred to, in which both common and olfactory sensibility were abolished by the cerebral lesions, no lacrymation was caused by acetic acid. In the other nostril, which had not lost its common sensibility, lacrymation was caused by acetic acid. But lacrymation may be caused by irritation of the nerves of common sensibility alone. Where

[1] *Brit. Med. Journal*, April 1864. See also three cases reported by Hughlings-Jackson, in which, however, it is not stated precisely in which nostril the defect was specially observed (*Lond. Hosp. Reports*, vol. i. p. 410).

[2] *Leçons sur les Fonctions et les Maladies du Système Nerveux*, tome ii. Leçon 15e.

common sensibility is abolished the effect must be attributed to the olfactory nerve.

PART IV.—*The Centre of Common or Tactile Sensibility.*

§ 23. In my earlier experiments,[1] which I have since abundantly confirmed,[2] I could discover no sign of impairment or loss of tactile sensibility after the most extensive lesions involving the convex aspect of the cerebral hemisphere. And yet, considering the definite localisation of the centres of sight, hearing, smell, and probably taste, as well as the respective motor centres, no conclusion seems *a priori* better warranted than that there must be a definite region for the various forms of sensibility included generally under the sense of touch (contact, pressure, temperature, &c.)

For up to the point of radiation into the cerebral cortex the sensory paths have been proved to be entirely differentiated from the motor; and that the two should become jumbled together indiscriminately in the cortical centres is a hypothesis which *prima facie* is extremely unlikely. The sensory nerve roots are entirely distinct from the motor, and in the spinal cord itself the sensory and motor centres and tracts are clearly differentiated from each other, as evidenced by the facts of anterior poliomyelitis, and by such cases as the remarkable one recorded by Spath-Schüppel.[3]

In the pons, and in the crura cerebri, it is rare to find lesions so limited as to affect the sensory tracts apart from the motor, though the occurrence of motor paralysis from lesions in these regions, without paralysis of sensation, shows that the sensory and motor tracts still retain their independence.

But we have ample proof both experimental and pathological that the sensory tracts of the internal capsule are quite distinct from the motor, and may be injured or diseased separately, with the result of causing hemianæsthesia on the opposite side of the body. It is evident that the cause of the

[1] *Philosoph. Trans.* vol. clxv. Part II. 1875.
[2] *Ibid.* Part II. 1884.
[3] *Archiv d. Heilkunde*, 1874, vol. xv. p. 44. Referred to Chap. IV. § 18.

hemianæsthesia in such case is not due to injury of centres, but merely to interruption of the paths of transmission from the periphery to the cortical centres. What remains, therefore, to be discovered is the cortical destination of these paths of common or tactile sensibility.

Anatomically the position of the sensory region of the internal capsule corresponds to the posterior third, or more, of the hinder division of the internal capsule, as seen in horizontal section (see fig. 25) lying between the optic thalamus and lenticular nucleus of the corpus striatum.

The experiments of Veyssière [1] have shown that when this portion of the internal capsule is divided in the brain of the dog (fig. 102) hemianæsthesia is produced on the opposite side of the body.

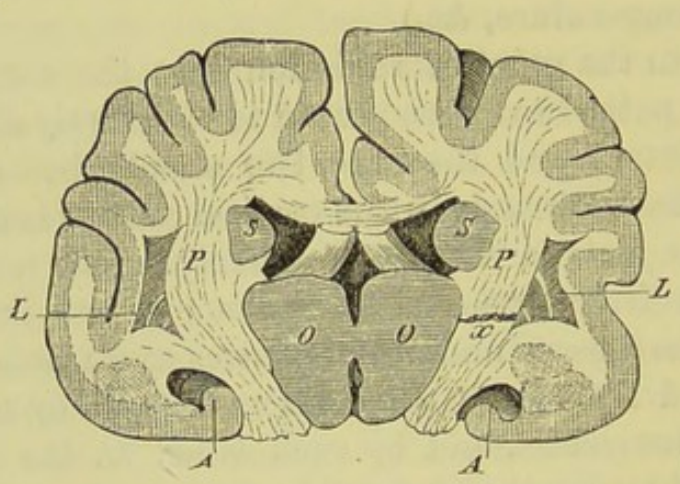


FIG. 102.—Vertical Transverse Section through the Brain of the Dog on a level with the Corpora mammillaria (Carville and Duret). OO, the optic thalami. SS, the nuclei caudati of the corpora striata on each side. LL, the lenticular nuclei of the corpora striata. PP, the internal capsule, or peduncular expansion. AA, the hippocampi. X, section of the posterior part of the peduncular expansion, causing *hemianæsthesia*.

Disease of the same region in man produces precisely similar results.[2] In this condition sensation, general and special, is abolished on the opposite side of the body, but the power of voluntary motion is retained—if the lesion does not also implicate the motor tracts. But though volitional movements are capable of being effected, all sense of movement is lost, nor does the most powerful contraction of the muscles

[1] *Recherches Cliniques et Expérimentales sur l'Hémianesthésie de Cause Cérébrale*, 1874.

[2] Charcot, *Le Progrès Médical*, 1875; Reymond *ibid.*; Rendu, *Des Anesthésies Spontanées*. Thèse, Paris, 1875.

induced by the electric current rise into consciousness. There is no sense of locality, or of the state of contraction of the muscles, and though the limb may be moved freely by the agency of the motor centres, it can only be used with purpose, and directed under the guidance of the eye, which enables the individual to place the limb in such positions as previous experience has associated with the accomplishment of certain desired effects. The directing agency of the eye being withdrawn, the position of the limb may become altered unconsciously, and a weight previously supported will fall to the ground; a fact of which the individual only becomes aware by other channels of perception. The following description by Demeaux[1] of a woman affected with cerebral hemianæsthesia is one which graphically represents the condition. 'She moved the limbs voluntarily, but she had no sense of the movements effected. She did not know in what position her arm was, nor could she tell whether it was flexed or extended. If she were asked to touch her ear, she immediately executed the proper movement, but if my hand were interposed between hers and her ear she was quite unconscious of the fact; and if I arrested her movement in mid-career she was utterly unaware of it. If I fixed her arm to the bed without her knowledge, and asked her to raise it to her head, she made an effort, and then ceased, believing that she had done what was wanted. If I told her to try again, pointing out that her arm had not been moved, she made a greater effort, and only when she had to throw the muscles of the other side into action did she become aware that some obstacle had been interposed.' These facts show clearly that the same condition which abolishes cutaneous sensibility also entirely annihilates the so-called muscular sense.

§ 24. From such and similar cases, many of which I have myself seen and investigated, and multitudes of which are to be found in medical literature, it is plain that the sensory tracts of the internal capsule are entirely distinct from the motor, and that there is no necessary relation between the power of effecting movement and the sense of movement effected. In other words, the paths of the so-called muscular

[1] Thèse, Paris, 1843, p. 100

sense are quite distinct from the paths of volitional impulse. Whether this holds also in respect to the centres will form the next subject of inquiry. Do the sensory tracts, which, up to the internal capsule, have maintained a separate position, fuse in the cortex with the motor, as some believe; or are they distributed to a special region of the cortex? Flechsig believes that the tracts which form the posterior or sensory division of the internal capsule are derived, through the tegmentum, from the sensory tracts of the formatio reticularis and lemniscus, and are distributed to that portion of the brain lying between the fissure of Rolando and the occipital lobe. But there is a tract occupying the outer third of the foot of the crus which was regarded by Meynert as the upward continuation of the posterior columns of the spinal cord, and therefore probably the paths of tactile or common sensibility. The posterior columns of the spinal cord, however, are not the paths of tactile sensibility (see Chapter II. § 7), nor does it appear that any direct connection can be considered as established between the outer third of the foot of the crus and these columns. Flechsig, however, is unable to trace this tract beyond the pons, but he is of opinion that it consists of fibres which connect the cerebrum with the cerebellum, as it was absent in a case in which the cerebellum was deficient. The same tract was also absent in a case of defective development of the brain reported by Starr.[1] But as in Starr's case the whole foot of the crus was absent also, and the cerebellum showed no defect, it is obvious that no relationship is established between the cerebellum and this tract.

That the tracts, forming the outer third of the foot of the crus, are centripetal in function is evident from the fact that they are never the seat of descending degeneration, like the inner two thirds; and, though no one has as yet succeeded in tracing their lower relations satisfactorily, the probability is that they are the more or less direct continuations of the sensory tracts of the spinal cord. This conclusion is especially supported by the anatomical distribution of these fibres in

[1] 'The Sensory Tract in the Central Nervous System,' *Journal of Nervous and Mental Disease*, July 1884.

the cortex. The tracts forming the outer third of the foot of the crus diverge from the internal capsule at the base, and radiate outwards and downwards towards the hippocampal region,[1] where, as will be seen, lesions invariably affect tactile sensibility.

§ 25. In my earlier experiments I had observed that, though tactile sensibility appeared entirely unaffected by lesions invading the convex aspect of the hemisphere, yet in certain experiments where the temporo-sphenoidal lobe was deeply injured (see Section III.) tactile sensibility became very much impaired, or altogether abolished on the opposite side of the body. In all these cases it was found, on post-mortem examination, that the hippocampal region—including the cornu Ammonis and gyrus hippocampi—was more or less extensively invaded. These facts strongly pointed to the hippocampal region as the seat of tactile sensibility, and I therefore devised experiments with a view to destroy this region primarily. To do so without injuring the occipital lobe or the convex aspect of the temporo-sphenoidal lobe is, however, impossible; but as the effects of lesion of the occipital lobe and of the inferior temporo-sphenoidal convolutions are readily capable of determination by themselves, it is a matter of no great difficulty to eliminate these in cases of lesion invading also the hippocampal region.

I have effected destruction of the hippocampal region, more or less completely, both by the method of penetration by means of a wire cautery, directed through or underneath the occipital lobe, and by cutting from the outer aspect of the inferior temporo-sphenoidal region inwards towards the hippocampal gyrus, so as to destroy or detach it, without injury to the crus cerebri or neighbouring structures.[2]

In one case[3] a wire cautery was thrust through the posterior extremity of the left occipital lobe, with a view to

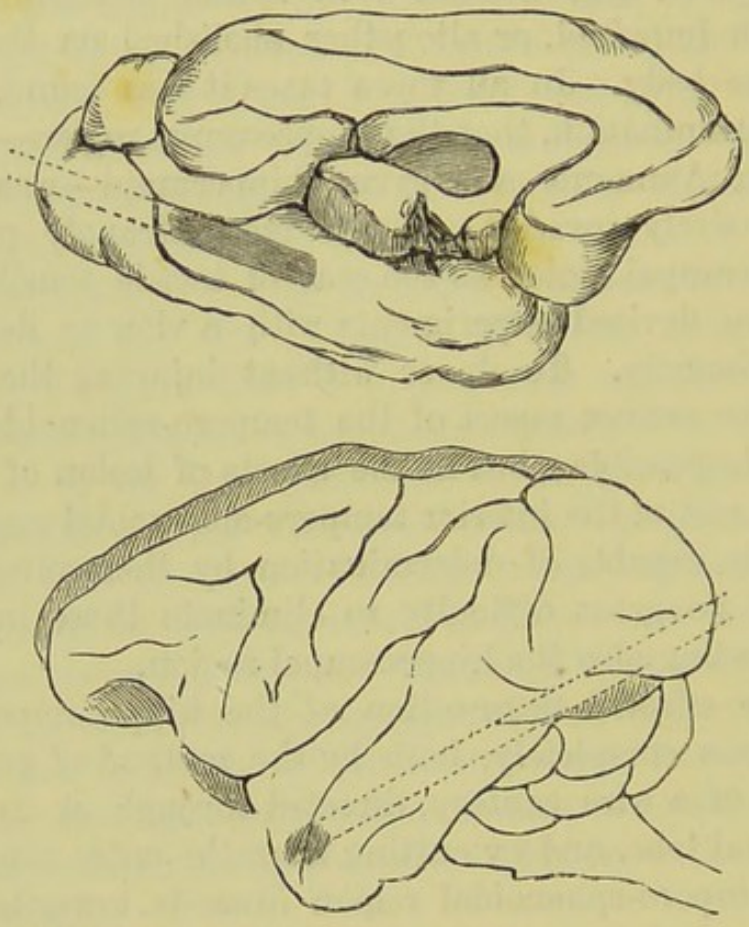
[1] Flechsig, *Plan des menschlichen Gehirns*, 1883, p. 17.

[2] See *Phil. Trans.* Part II. 1884, Section V. figs. 87–181.

[3] Experiment XVII., *Phil. Trans.* Part II. 1875, figs. 22 and 23. Though in this case there were some indications of basal meningitis, this had not occurred to such an extent as to result in any softening or actual lesion beyond that caused by the cautery.

traverse the hippocampus. In reality it proved, on post-mortem examination, that the cautery had swerved too far outwards, and just missed the hippocampus itself. Immediately after the operation, and for two days subsequently, there was no defect of tactile sensibility; but on the third day this became so much impaired that scarcely any reaction was induced by a degree of heat which excited most lively signs of sensation on the left side.

It was found after death that the track of the cautery,



FIGS. 103 and 104.—Fig. 103, Internal Aspect, and fig. 104, External Aspect of the Left Hemisphere, showing the track of the cautery in the experiment described in the text.

which had primarily passed outside the hippocampus (figs. 103, 104), had become the centre of secondary inflammation, which had extended into, and softened, the hippocampal region.

In a second experiment[1] a wire cautery was similarly pushed through the tip of the right occipital lobe along the

[1] Experiment XVIII., fig. 24, *Phil. Trans.* Part II. 1875.

hippocampal region—this time, as proved after death, with perfect success, and without injury to other structures. The effects of this lesion were very striking.

The monkey in question, which was the subject of the present experiment, was found to be, as a rule, left-handed, taking things offered to it preferably with the left hand. For this reason the right hippocampal region was destroyed, with the view of affecting the sense of touch in the limb which the animal usually employed.

After recovery from the operation and the narcotic stupor, sight and hearing were found to be unimpaired, and the intelligence quick and active as before. But cutaneous stimulation by pricking, pinching, or pungent heat sufficient to cause lively manifestations of sensation when applied to the right

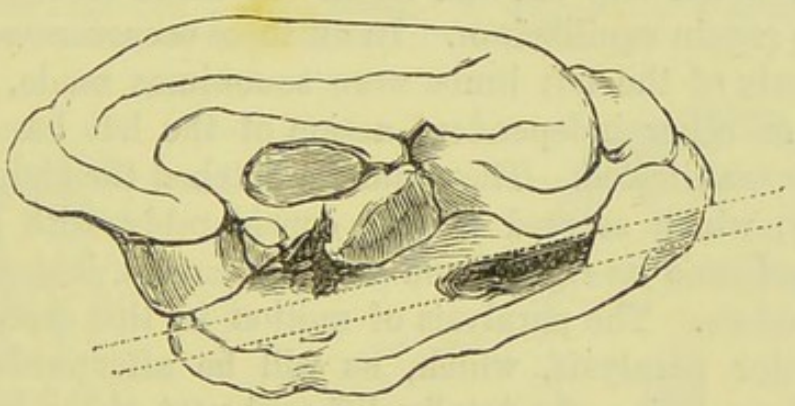


FIG. 105.—Internal Aspect of Right Hemisphere of Brain of Monkey. The shading and dotted lines indicate the track of the cautery and position of the lesion, causing loss of tactile sensation on the left side of the body. (Roy. Soc.)

side of the body, failed in general to elicit any reaction whatever on the left side, whether face, hand, or foot. Only occasionally, when the stimulus was intense or long continued did reaction at all ensue. This most remarkable absence of response of any kind of itself satisfactorily proved the fact of annihilation of tactile sensibility without further evidence. But the abolition of tactile sensation was further conclusively shown by the condition as to motility of the left limbs. There was no flaccidity of the muscles, and no facial distortion, as is observed in motor hemiplegia; but the arm was kept motionless by the side, and the leg straddled outwards, or was placed irregularly, and yet a certain amount of voluntary control was retained over the limbs. This was ex-

emplified by the following incident which occurred in the course of the observations :—

On being placed within its cage the animal mounted its perch, gaining its position with some difficulty, on account of its tendency to fall over on the left side. While endeavouring to turn on its perch the left foot slipped off, whereupon, in the struggle to recover its equilibrium, the animal clutched with both hands at the bars of the cage, but grasped only with the right hand, the left being powerless. Aided by its teeth and right hand, it recovered its position, and after grasping the perch firmly with its right foot ultimately dragged up the left leg. This position of steadiness, however, was possible only while the animal kept on the alert. On its dropping off to sleep, which it continually tended to do, the left foot would slip off, and again the same struggle would occur to regain equilibrium. In all these occurrences, though movements of the left limbs were sometimes made, no prehensile or other independent action of the left hand or leg was ever manifested. The animal scratched the right side of its body, which seemed to itch considerably, with its right hand, and used its right hand for prehension, instead of the left as before. The paralysis of motion in this case was not true motor paralysis, which, as will be afterwards shown, results from lesion of a totally different part of the brain, but the paralysis of motion which is due to the loss of tactile sensation, by which movements are guided.

The animal was killed with chloroform on the same day in order that the position and extent of the primary lesion might be determined before secondary softening could occur. As already stated, the lesion was confined to the hippocampal region, along which the cautery had ploughed its way with great precision. As the position of the lesions in these two cases had been questioned, and a suggestion made that in reality the internal capsule had been injured, I carefully re-examined the brains, which had been carefully preserved n spirit. The accompanying figures (figs. 106, 107), drawn from nature, show the exact appearances presented in the two cases. A series of frontal sections,[1] of which fig. 108 is one

[1] See photographs, figs. 87–102, *Phil. Trans.* Part II. 1884.

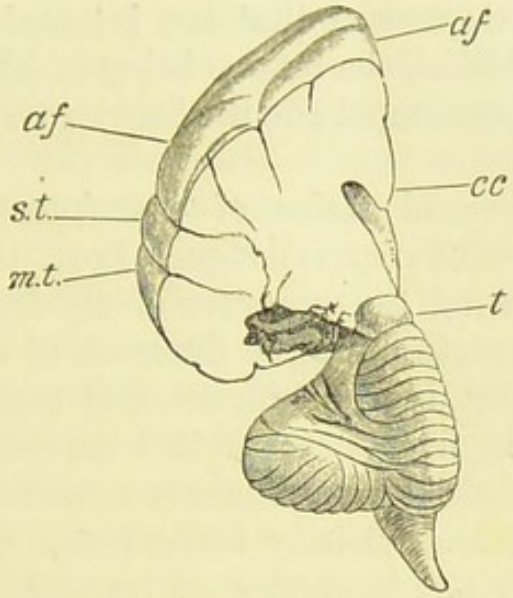


FIG. 106.—Natural appearance of Brain represented in diagrams 103, 104, the posterior lobe being removed. On the upper aspect of the left lateral lobe of the cerebellum there is a superficial groove where it was grazed by the cautery.—*af*, ascending frontal convolution. *cc*, corpus callosum. *mt*, middle temporo-sphenoidal convolution. *st*, superior temporo-sphenoidal convolution. *t*, testes.

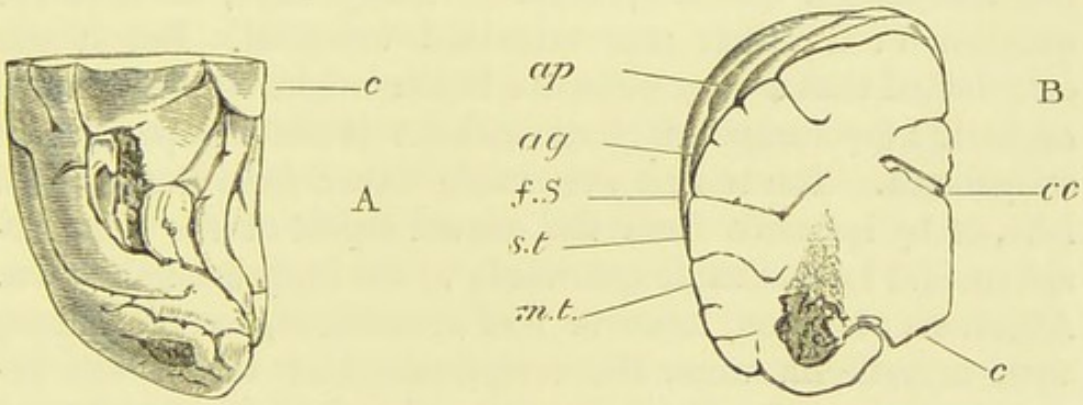


FIG. 107 (A, B).—Natural Appearance of Posterior Half of Right Hemisphere represented in diagram fig. 104.—A, under surface. B, seen from before. The position of the lesion is clearly indicated by the shading. *c*, crus cerebri. *cc*, corpus callosum. *ag*, angular gyrus. *ap*, ascending parietal convolution. *fS*, fissure of Sylvius. *mt*, middle temporo-sphenoidal convolution. *st*, superior temporo-sphenoidal convolution.



FIG. 108.—Frontal Section of fig. 107, B, showing the Destruction of the Hippocampal Region. (After a sun-print.)

of the second case, showed that the internal capsule was entirely free from lesion, the lesions being in both cases strictly limited to the hippocampal and the inferior temporo-sphenoidal region.

§ 26. In a second series of experiments[1] made partly in conjunction with my colleague, Prof. G. F. Yeo, with the object of testing the accuracy of my former results, and also in order to determine the duration of the symptoms, I established lesions in the hippocampal region in ten other monkeys, and in five of these in both hemispheres. The results of this series of experiments confirmed in every particular those I had already arrived at, and showed that tactile sensibility was in every case impaired or abolished in proportion to the amount of destruction of the hippocampal and inferior temporo-sphenoidal region. Unfortunately none of the animals in which the destruction was complete, and the anæsthesia absolute, survived many days, so that the question of duration still remained unsolved. But it was established that a very extensive lesion might be made in one or both hippocampal regions without producing permanent anæsthesia. The lesions were made either from the occipital lobe, or by incisions from the convex aspect of the temporo-sphenoidal lobe, extending inwards to the hippocampal region. Affections of vision, more or less evanescent, occurred along with anæsthesia when the occipito-angular region was invaded, in accordance with the facts stated in Section I., and occasionally some affection of hearing occurred when the superior temporo-sphenoidal convolution was involved. But it was only when the hippocampal region was injured that anæsthesia showed itself.

In one experiment[2] the animal had been previously rendered partially hemiplegic on the left side by lesion of its right Rolandic zone (see Chapter X. p. 354). Lesion of the left hippocampal gyrus induced profound impairment of the sensibility of the whole of the right side of the body, and it was interesting to note how the slightest touch on the paralysed limbs immediately attracted the animal's attention, whereas

[1] *Phil. Trans.* Part II. 1884. Experiments 24–33, figs. 103–181.

[2] Experiment 24, figs. 103–109, *Phil. Trans.* Part II. 1884.

not the slightest sign of perception was elicited by the same kind of stimulation on the other side. In this case the anæsthesia, which did not amount to insensibility to painful stimulation, gradually disappeared, and ceased to be capable of detection a week after the operation.

In a second experiment[1] a wire cautery was directed through the occipital lobe in the line of the collateral fissure, and following the course of the descending cornu of the lateral ventricle, detaching and destroying a considerable extent of the medullary fibres of the hippocampal gyrus. The result of this lesion was temporary hemiopia to the left side, and a condition of total anæsthesia to mere contact. This showed signs of retrogression at the end of a few days, but the impairment of tactile sensibility still continued very evident for a fortnight after the operation. At first the fingers and toes of the left side could be touched or gently scratched without in the least exciting the animal's attention, whereas similar stimulation of the extremities on the right side invariably caused the animal to look and to change its position.

A month after the infliction of the injury on the right hippocampal region a similar lesion, but somewhat more extensive, was established on the left side. This operation also severed the portion of the optic tract passing to the corpus geniculatum externum. The animal became absolutely hemiopic to the right side, and continued so till death, nearly a year and a half after the operation. Tactile sensibility was completely abolished in the limbs of the opposite side; and it was noted that the lesion did not reinduce the anæsthesia on the left side, which had been the result of the lesion of the right hemisphere. Sensibility gradually returned in the right limbs, but some impairment of perception of mere contact was observable for a month after the operation, and particularly in the foot.

The defect as regards vision seen in this animal is explained first by the lesion of the right occipito-angular region, and second by the direct lesion of the optic tract on the left, which was the cause of the permanent right hemiopia. But the affection of tactile sensibility, first on the one side and

[1] Experiment 25, figs. 110–116, *op. cit.*

then on the other, was clearly the result of the injuries inflicted on the hippocampal region : the ganglia, crura cerebri, and internal capsule being absolutely intact.

In a third experiment [1] first the left, and, three weeks subsequently, next the right hippocampal region were partially destroyed by heated wires thrust through the occipital lobes. Owing to the injuries of the medullary fibres of the occipito-angular regions vision was impaired. The lesion in the left hemisphere only divided a portion of the medullary fibres of the hippocampal gyrus, and there was only slight and transient impairment of tactile sensibility on the right side. In the right hemisphere the gyrus hippocampi was peeled off, leaving the cornu Ammonis itself and its connections apparently intact. As the result of this there was complete tactile insensibility on the left side, which, however, gradually diminished, and could no longer be detected ten days after the operation.

In a fourth experiment [2] the whole of the inferior temporo-sphenoidal convolution and portion of the middle temporo-sphenoidal convolution of the right hemisphere were cut away, and considerable injury inflicted on the medullary fibres of the hippocampal region. After this lesion there was considerable, but not total, analgesia to severe thermal stimulation on the left side, but total insensibility to mere contact, so that the hand or foot could be touched or rubbed without the slightest sign of perception on the part of the animal. Sensibility gradually returned, however, so that at the end of a fortnight it was impossible to detect any difference between the tactile perception of the two sides. At the end of this time a wire cautery was pushed through the convexity of the left occipital lobe, so as to traverse and destroy the cornu Ammonis and medullary fibres of the gyrus hippocampi, as well as those of the inferior and middle temporo-sphenoidal convolutions. The cortex of the gyrus hippocampi formed merely a thin shell enclosing the broken-down *débris* of the cornu Ammonis and the medullary substance. After this there was almost complete analgesia, as tested by severe thermal stimulation, on the right side, and total anæsthesia

[1] Experiment 26, figs. 117–124, *op. cit.*

[2] Experiment 30, figs. 149–156, *op. cit.*

to mere tactile stimulation, such as touch, rubbing, &c. of the limbs. The permanency of these symptoms, however, could not be determined, as the animal passed into a state of coma on the following day, and was killed with chloroform. In this animal motor power, hearing, and vision were unimpaired from the first.

In a fifth experiment[1] the inferior temporo-sphenoidal and greater portion of the hippocampal region of the left hemisphere were destroyed. When the animal had entirely recovered from the operation it was found that there was almost complete analgesia of the right side and complete tactile anæsthesia. The anæsthesia affected also the cutaneo-mucous surfaces, so that the right nostril could be tickled without causing any reaction, whereas the same stimulation of the left caused grimaces and evident signs of uneasiness. So also the right side of the tongue could be touched and pricked without any signs of reaction; whereas the same stimulation of the left side caused the animal to rub the part. All the volitional movements of the right side were retained, but the animal tended constantly to fall over on the right side, evidently owing to the loss of the so-called muscular sense.

This animal died suddenly on the day following the operation from secondary hæmorrhage, so that no further observations as to the permanency of the symptoms were possible.

In a sixth experiment[2] a wire cautery was so directed, underneath the left occipital lobe downwards and forwards, as to pass along the dentate fissure, and shear off the fascia dentata and portion of the alveus of the cornu Ammonis, in a most remarkable manner, without injury to the optic tract or other structures. The effect of this limited, and apparently impracticable, lesion was a well-marked hyperæsthesia, instead of anæsthesia, over the whole of the opposite side of the body, so that the signs of sensation to various forms of stimulation, such as plucking the hairs, were very much more energetic than on the left side.

This condition had quite disappeared on the day following the operation, and the animal appeared in other respects, with

[1] Experiment 31, figs. 157–163.

[2] Experiment 32, figs. 164–172, *op. cit.*

the exception of slight defect of vision to the right, perfectly normal. On the tenth day no impairment of vision could be any longer made out.

In this case the lesion seems only to have excited the centres of tactile sensibility, probably by throwing the hippocampal region, which was only very slightly injured, into a state of active congestion or irritation. A month after the first operation the right temporo-sphenoidal lobe was exposed, and severed in such a manner by incisions as to detach the lower half of the middle and inferior temporo-sphenoidal convolutions, and break up to a considerable extent the medullary fibres of the corresponding portion of the hippocampal region. Superficially, however, the whole of the gyrus hippocampi was perfectly intact, the incisions not extending inwards beyond the collateral fissure.

As the result of this lesion there was a considerable degree of analgesia on the opposite side, and complete insensibility to mere tactile stimulation, so that the limbs could be touched, rubbed, and the hair ruffled without causing the slightest sign of perception; whereas the same stimulation on the right side caused the animal to put its hand or foot to the place. In doing so, it at first generally fell over on the left side. The left nostril could also be tickled without causing any sign of uneasiness, while on the right the same proceeding caused an active grimace. Vision and hearing, and the motor powers, were altogether unimpaired. On the third day after the operation the tactile anæsthesia was less pronounced, and it gradually diminished, so that at the end of a week it was no longer perceptible. From this time onwards, till its death by chloroform two months subsequently, the animal appeared in perfect health, and without discoverable defect either as regards general or special sensibility or motor powers.

In a seventh experiment [1] the left cornu Ammonis was disorganised from end to end, in the most precise manner, by means of a wire and porte caustique directed through and beneath the extremity of the occipital lobe, leaving the gyrus hippocampi and its medullary connections intact. The animal was able within an hour to move about, planting its right

[1] Experiment 33, figs. 173 181.

limbs in a very awkward and uncertain manner, but without any appearance of motor paralysis. There was profound, almost complete, analgesia of the limbs on the right side, and total insensibility to mere tactile stimuli. There was also anæsthesia of the right nostril, so that no notice was taken when the interior was tickled. The analgesia had disappeared on the following day, but the anæsthesia to touch, &c. continued. This, however, also gradually disappeared, and was no longer perceptible on the fourth day. There was, however, complete right hemiopia, which was found to be dependent on lesion of the left optic tract, which had been grazed and almost completely severed.

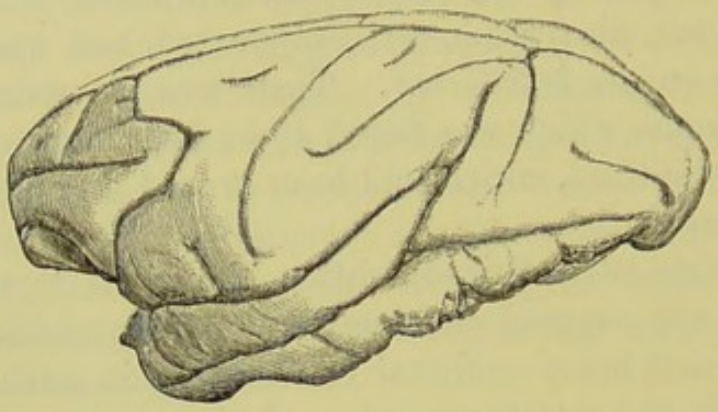
A fortnight after this operation the right temporo-sphenoidal lobe was exposed and incised along the middle temporo-sphenoidal and lower occipital convolution in such a manner as to detach the greater portion of the temporo-sphenoidal region, included between these incisions, from the rest. The incisions were such as to sever the medullary connections of the hippocampal region, especially towards the anterior or lower half. Almost complete analgesia was observed in the limbs of the left side, but the animal died on the following day before further observations could be made.

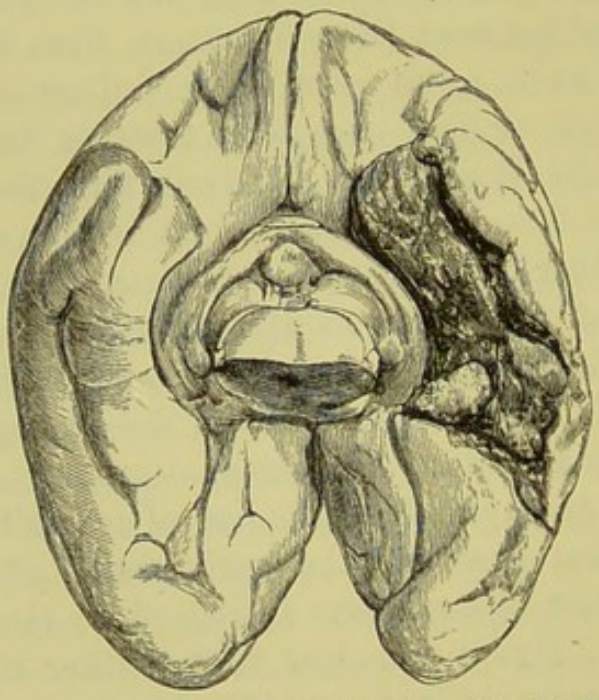
In none of the above-mentioned experiments was the analgesia absolute from the first, and in none of them did the destructive lesion involve the whole of the hippocampal region —hippocampus as well as hippocampal gyrus.

In those of them in which the loss of sensibility to painful stimuli was most complete the early death of the animals prevented further observations in regard to the duration of the symptoms. But it was clear that neither destruction of the gyrus hippocampi alone nor of the hippocampus alone was sufficient to induce permanent anæsthesia on the opposite side. In each case, however, whether the lesion involved the gyrus hippocampi, or hippocampus alone or mainly, there was pronounced affection of tactile sensibility, and the degree and duration of the anæsthesia were in proportion to the extent of injury inflicted. In the remarkable case, however, of the sixth animal the slight lesion of the fascia dentata caused an extraordinary hyperæsthesia instead of a diminution of tactile

sensibility; but this, as has been remarked, was an irritative rather than destructive lesion of the hippocampal region, and the true counterpart of the others, and thus quite harmonising with them.

In an eighth and ninth experiment greater success was obtained in respect to the completeness of the destruction of the





FIGS. 109 and 110.—Fig. 109 shows the Lateral Aspect, and Fig. 110 the Under Surface of the Left Hemisphere in a case of Lesion, causing complete anæsthesia of the opposite side of the body. (From photographs.)

hippocampal region and the profoundness of the anæsthesia; but unfortunately the observations as to the duration of the effects were cut short by the sudden death of the animals a few days after the operation in each instance.

In the eighth experiment[1] the left hemisphere was exposed,

[1] Experiment 27, figs. 125–132, *op. cit.*

and the whole of the inferior temporo-sphenoidal convolution and hippocampal region were severed and scooped out, the lesion being such as to leave only the internal margin of the gyrus hippocampi with the tænia semicircularis and the fimbria of the fornix intact (see figs. 109, 110). Only a portion of the hippocampal gyrus included between the calcarine and collateral fissure (lingual lobule) remained.

The result of this experiment was most striking. There was, on the right, complete insensibility to thermal stimulation of such intensity as to cause the most lively sensations of pain on the left side, and total insensibility to every form of mere tactile stimulation, such as touching, gentle pricking, rubbing, &c. The limbs were capable of being freely moved volitionally, but they were planted with great awkwardness and uncertainty as to position.

While the animal was resting, with its eyes shut, I drew the right arm away from the side, without its seeming to be aware of the fact, until it fell over. It was keenly sensitive to every form of stimulus, however slight, on the left side. Hearing was unimpaired on both sides. Vision, however, appeared somewhat indistinct, though not abolished, towards the right. There was also anæsthesia of the right nostril.

The symptoms remained unchanged on the second day after the operation, the animal being otherwise in apparent perfect health and vigour, but on the third day it died suddenly from secondary hæmorrhage.

A series of microscopic sections [1] of the brain showed that, with the exception of the injuries above described in the inferior temporo-sphenoidal and hippocampal region, the basal ganglia, crura cerebri, and other structures were perfectly intact.

In the ninth experiment [2] a similar lesion was established in the left hemisphere, involving almost complete detachment of the hippocampal and lower temporo-sphenoidal region from the rest of the hemisphere. In this animal also there was at first almost if not total analgesia, and absolute anæsthesia to all gentle forms of tactile stimulation, over the whole of the

[1] See figs. 127–130, *op. cit.*

[2] Experiment 28, figs. 133-140.

right side of the body. Hearing was unimpaired on the right, but vision was somewhat defective towards this side, the animal appearing to have only some degree of uncertainty as to the position of things offered it on the right front. The condition remained practically unchanged on the third day, when the animal had a slight unilateral right-sided fit, lasting a few seconds, indicating some irritation—as was found after death—caused by slight secondary hæmorrhage. After this the analgesia became absolute, and no sign of perception could be obtained to any form of tactile stimulation. The animal could move its limbs freely, and lay hold of objects firmly with the right hand, but it continually fell over on the right side, owing to the awkward and uncertain manner in which it planted its limbs. There was also total insensibility to tickling of the right nostril. The same stimulation of the left caused active grimaces and signs of uneasiness.

Death occurred on the fourth day from secondary hæmorrhage. The lesion was found accurately limited to the lower temporo-sphenoidal and hippocampal region of the left hemisphere, without the slightest implication of the crus or basal ganglia.

In a tenth experiment[1] a similar lesion of the inferior temporo-sphenoidal and hippocampal region produced exactly similar results, there being almost complete analgesia, and absolute tactile anæsthesia over the whole of the opposite side. In this case also, however, sudden death occurred on the third day, rendering further observations as regards the permanency of the effects impossible.

§ 27. The foregoing experiments demonstrate the fact that the various forms of sensibility embraced under the term common or tactile sensibility—including cutaneous, mucocutaneous, and muscular—are capable of being profoundly impaired or altogether abolished, for the time at least, by destructive lesions of the hippocampal region; and the degree and duration of the anasthesia vary with the completeness of destruction of the region in question.

We have seen that lesions of the gyrus hippocampi alone, and of the hippocampus itself alone, do not produce permanent

[1] Experiment 29, figs. 141–148.

effects. But whether recovery may ensue after complete removal of both is a point which unfortunately the fatality of the operations in my hands rendered it impossible for me to determine by my own experiments, so far as I had been able to carry them. I have, however, had the great advantage of witnessing and studying the effects of similar operations carefully planned and skilfully conducted by Professors Horsley and Schäfer, which have succeeded in throwing much additional light on the subject, and deciding certain doubtful points. In these experiments the lesions were established, under strict antiseptic precautions, by excision with the scalpel, so as to obviate all possible risk of diffuse effects. In order to reach and remove the hippocampal region the temporo-sphenoidal lobe was exposed, and the convexity removed in such a manner as that the hippocampus and hippocampa gyrus could be clearly displayed and removed *en masse* without any injury being inflicted on the crus cerebri.

In one animal in which this operation was effected there was on the following day partial analgesia, and complete insensibility to mere contact, on the opposite side. Death, however, occurred on the second day, so that no further observations as to duration were possible in this case.

In a second experiment the hippocampal region was removed, and the incisions made so as to detach also the margins of the calcarine fissure and hippocampus minor. This animal was profoundly anæsthetic on the opposite side, but there did not appear to be absolute analgesia. All mere tactile stimuli, however, like touch, scratching, rubbing, gentle pricking, was absolutely unperceived, while similar stimulation on the other side at once attracted attention.

The condition of tactile anæsthesia continued for several weeks without appreciable alteration, but a gradual improvement occurred, so that examination at the end of six weeks revealed only some degree of impairment, as evidenced by less easily excited attention on gentle pricking, rubbing, &c. of the side opposite the lesion, as compared with the other. Severe pricking, pinching, or pungent heat, however, appeared to be well perceived.

The observations on the degree of recovery after apparently

total extirpation of the hippocampal region led to the idea that probably the sensory region included also the callosal division of the falciform lobe, and to test this hypothesis the following experiment was performed.

In an animal in which, some weeks previously, the hippocampus had been removed, and which had completely recovered from any anæsthesia which might have existed directly after the operation, the same hemisphere was again exposed in the region of the longitudinal fissure, and the gyrus fornicatus excised along the whole length of the corpus callosum.

The effect of this second operation was to cause absolute analgesia on the opposite side, continuing for several days after the operation, as well as complete insensibility to all milder forms of tactile stimulation. The analgesia diminished somewhat as time went on, but six weeks after the operation it was still manifest in some degree. The tactile anæsthesia was, however, apparently in nowise improved, all gentle forms of tactile stimulation being absolutely unperceived. The animal was in perfect health, and exhibited no indications of motor disorder; though directly after the operation there was slight weakness of the opposite leg, owing to the rather rough handling of the postero-parietal lobule and neighbourhood during the operations necessary to expose the gyrus fornicatus.

This experiment completely verified the hypothesis which led to its being made, viz. that the gyrus fornicatus forms part of the tactile sensory centre, and is a physiological demonstration of the accuracy of the anatomical views of Broca that the callosal and hippocampal regions form part of one great and distinct lobe—the falciform lobe. But at the same time it demonstrates the inaccuracy of his hypothesis, that the falciform lobe is related only to the sense of smell, and varies with the development of the olfactory bulb. It has already (p. 314) been seen that the callosal division of the falciform lobe bears no relation to the development of the olfactory bulb, inasmuch as it is more than usually developed and convoluted in the cetaceans, which have no olfactory bulb, or only a very rudimentary one. The only undoubted relationship is between the development of the olfactory bulb and the hippocampal lobule, or region of the nucleus amygdalæ.

The rest of the falciform lobe forms the centre of common or tactile sensibility.

Therefore, in addition to the hippocampal region proper, we must include the callosal gyrus as forming part of the common sensory centre. This will explain the gradual restitution of tactile sensibility in those cases in which, notwithstanding the extensive, if not complete, destruction of the hippocampal region, the anæsthesia, at first pronounced, gradually disappeared. For in this case, as in other centres, a portion is capable of carrying on the functions of the whole.

The further experiments of Horsley and Schäfer have proved that removal of the gyrus fornicatus alone produces effects like those caused by removal of the hippocampal region, viz. a more or less enduring analgesia and anæsthesia of the opposite side of the body. Partial lesions of this gyrus may, however, be made without producing any obvious deficiency. Thus in an animal in which the quadrilateral lobule alone was removed, after removal of the occipital lobe some time previously, we were unable to detect any impairment of tactile sensibility. This is in harmony with the fact, copiously illustrated in the foregoing experiments, that partial lesions only of the hippocampal region, cornu Ammonis or gyrus hippocampi, produce only transient anæsthesia. The whole of the experiments, however, taken together, clearly prove that the centres of common sensibility are situated in the falciform lobe, and that, to produce absolute and permanent anæsthesia, it is necessary to destroy the whole of this lobe, callosal as well as hippocampal division. This is not easily effected, owing to the extreme difficulty of completely exposing and extirpating the falciform lobe without causing serious complications or fatal injuries. But though up to the present the experiments have not furnished a case of absolute and permanent analgesia, as well as anæsthesia, they have furnished abundant evidence that the degree and duration of the anæsthesia are in proportion to the completeness with which this lobe has been removed ; a concomitant variation which establishes beyond all doubt that the falciform lobe is the centre of common and tactile sensation. The symptoms observed in the animals operated on prove that the centres of mere touch proper are precisely the same as

those of painful sensation—whether from pressure, heat, or otherwise—the latter being merely an intense degree of the former. In cases in which the lesions have not been sufficient to induce analgesia, they have, however, been sufficient entirely to annihilate mere tactile sensibility. In the same regions are also the centres of cutaneo-mucous and so-called muscular sensibility. In many of the cases the interior of the nostril, and the tongue, were found to be quite as anæsthetic as the skin; and that the so-called muscular sense was similarly affected was shown by the awkward use of the limbs, and the obvious insensibility to passive movements—so well exemplified in the ninth experiment above recorded.

The effects of destruction of the falciform lobe are exactly like those observed in hemianæsthesia of cerebral origin in all that relates to common sensibility. For here also there is analgesia or anæsthesia not only of the skin, but of the cutaneo-mucous membranes, together with loss of the so-called muscular sense. The falciform lobe, therefore, is the cortical centre of those fibres of the internal capsule, destruction of which is the cause of hemianæsthesia of organic origin.

I have not been able to satisfy myself as to the differentiation in the falciform lobe of centres of sensation for the different regions of the body, like that which is so characteristic of the motor zone. In general, where anæsthesia has been produced, whether from lesions of the hippocampal region alone or of the callosal gyrus, it has affected the whole of the opposite side, face, arm, trunk, and leg. Occasionally, however, it has seemed as if one region had been more affected than others, but at other times this has not been noted. Without pronouncing definitely on this point, I am inclined to think that the experimental evidence is against any absolute differentiation of centres of tactile sensation for special regions. One of the strongest arguments is the fact that recovery ensues throughout in time, even after the most complete destruction of one portion of the falciform lobe, as in one of Horsley and Schäfer's experiments; and in many of my own experiments, in which very extensive lesions were established in the hippocampal regions, the recovery was more rapid than could be accounted for on the supposition that the hippocampal region

constituted the whole of the sensory centre for any one particular region. All the facts receive the most satisfactory explanation, if we regard the falciform lobe as a whole, and in each and every part the centre of tactile sensation for the whole of the opposite side of the body ; though probably the various motor centres are each anatomically related by associating fibres with corresponding regions of the falciform lobe. This association would form the basis of a musculo-sensory localisation.

CHAPTER X.

THE HEMISPHERES CONSIDERED PHYSIOLOGICALLY.

The Motor Centres.

§ 1. It has been shown (Chapter VII.) that electrical stimulation of the brain of the monkey at certain definite points in the convolutions which, speaking generally, form the boundaries of the fissure of Rolando gives rise to definite and predictable movements of the trunk, legs, feet, arms, hands, facial muscles, tongue, &c., the centres being arranged in the order of enumeration from above downwards.

Similar, and in many respects precisely the same, movements were shown to result from irritation of the frontal divisions of the external convolutions in the carnivora, and of the anatomically corresponding frontal region of the smooth brain of the rodentia. In the various figures the regions characterised by similar movements have been indicated by the same letters of designation. As a basis of topographical homology between the brain of the monkey (and man) and the lower vertebrates these data have an important value. The crucial sulcus (fig. 73, B) has been regarded by some as the homologue of the fissure of Rolando. Others (Meynert, Pansch) regard the coronal fissure or anterior division of the superior external sulcus as the true homologue; while Broca finds it in the præ-Sylvian sulcus, or sulcus bounding the gyrus formed by the anterior extremities of the lower three external convolutions (fig. 73 in front of (9) (9)).

A serious objection to Broca's view is the fact that in this case the centre for the movements of the head and eyes (fig. 73 (12)), would be placed posterior to the fissure of Rolando, whereas in the monkey this centre is situated well in advance

of it. For this reason alone the homology of the præ-Sylvian sulcus with the fissure of Rolando is more than doubtful. Nor does the cruciate sulcus, which I was formerly inclined to regard as the homologue of the fissure of Rolando, appear truly to represent this fissure. The crucial sulcus is only the anterior extremity of the subparietal sulcus, which forms the superior boundary of the callosal gyrus in the internal aspect of the hemisphere, and is occasionally absent in the brain of carnivora. If, however, with Meynert and Pansch we take the coronal sulcus as the fissure of Rolando, it is possible to trace a very close correspondence between the position of the various centres in the monkey, cat, dog, and other animals. The differences which are found to exist in the movements excited from anatomically corresponding points are such as would be accounted for by the different habit and modes of activity of the animals. Thus the relatively large area devoted to the facial movements (fig. 73 (7)) in the dog might be looked upon as corresponding with hand movements of the monkey (fig. 70 (*a*), (*b*), (*c*), (*d*)), as represented in the ascending parietal convolution. And in the cat, in which the paw possesses highly differentiated movements, the centre for the protrusion of the claws and clutching action (fig. 77 (*a*)) corresponds very accurately with the position of the hand centre (fig. 70 (*a*)) in the brain of the monkey.

§ 2. As regards the physiological significance of these regions, we have seen that we cannot conclude from the mere occurrence of movement on the electrical stimulation that the regions are truly motor; for the stimulation of a sensory centre may give rise to reflex or associated movement. Thus, stimulation of the superior temporo-sphenoidal convolution, which we have found to be a purely sensory centre—the centre of hearing—almost invariably gives rise to movement of the auricle, as well as of the head and eyes.

Whether the centres now under consideration are directly motor, or only give rise to movements in a similar reflex, or indirect manner when stimulated, is a question which has been answered differently by different physiologists. The definite purposive character clearly perceivable in most of the movements, however, their correspondence with the ordinary voli-

tional activities and individual peculiarities of the animals, and above all their uniformity and predictableness, harmonise best with the hypothesis that they are the signs of the artificial excitation of the functional activity of centres immediately concerned in effecting volitional movements, and as such truly motor. If these centres are part of the mechanism of volitional movements, then paralysis of voluntary motion, and of motion only, ought to result from their destruction, and any apparent exception must be capable of satisfactory explanation in accordance with this view, if it is the correct one. The first experiment I made is illustrative of the effects of irritation, followed by destruction, of the convolutions bounding the fissure of Rolando.

The right[1] hemisphere of a monkey had been exposed and subjected to experimentation with electrical irritation. The part exposed included the ascending parietal, ascending frontal, and posterior extremities of the frontal convolutions. The animal was allowed to recover, for the purpose of watching the effects of exposure of the brain. Next day it was found perfectly well. Towards the close of the day following, on which there were signs of inflammatory irritation and suppuration, it began to suffer from choreic spasms of the left angle of the mouth and left arm, which recurred repeatedly, and rapidly assumed an epileptiform character, affecting the whole of the left side of the body. Next day left hemiplegia had become established, the angle of the mouth drawn to the right, the left cheek-pouch flaccid and distended with food, which had accumulated outside the dental arch, there being almost total paralysis of the left arm, and partial paralysis of the left leg. On the day following the paralysis of motion was complete over the whole of the left side, and continued so till death, nine days subsequently. Tactile sensation, as well as sight, hearing, smell, and taste, were retained. On post-mortem examination it was found that the exposed convolutions were completely softened, but beyond this the rest of the hemisphere and the basal ganglia were free from organic injury (fig. 111).

[1] 'Experiments on the Brain of Monkeys,' *Philosoph. Trans.* vol. clxv. Part II. 1875.

In this we have a case, first, of vital irritation, producing precisely the same effects as the electric current; and then destruction by inflammatory softening, resulting in complete paralysis of voluntary motion on the opposite side of the body without affection of sensation.

In the next experiment the lesion was more limited, and the state of paralysis was limited correspondingly. The left hemisphere of a monkey was exposed, and the cortical substance destroyed by the cautery in the postero-parietal lobule (foot centre), ascending parietal convolution (hand and wrist movements), and superior part of the ascending frontal convolution (movements of arm and leg) (see fig. 70).

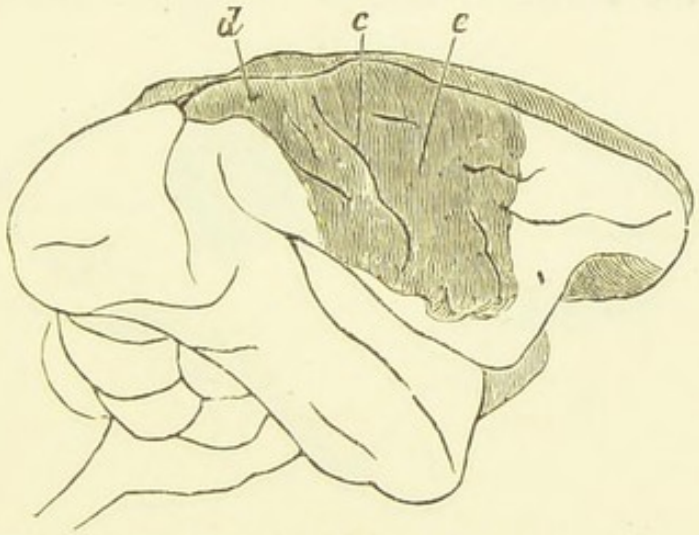


FIG. 111.—Lesion of the Grey Matter of the Right Hemisphere, causing complete hemiplegia of the opposite side without affection of sensation. (Roy. Soc.) *c*, the fissure of Rolando. *d*, the postero-parietal lobule. *e*, the ascending frontal convolution.

The centres of the biceps, facial muscles, and mouth and tongue were not involved. Immediately on this being done the right leg was found to be dragged, the foot and ankle especially hanging flaccid and powerless.

The right hand and wrist hung powerless and flaccid, but the animal could flex the forearm and maintain resistance against extension; a fact easily accounted for by the biceps centre remaining intact. There was no trace of facial paralysis or distortion of the angle of the mouth. Cutaneous sensation and the various special senses were unimpaired, and beyond the paralysis mentioned the animal was in good condition, and enjoyed food. In this animal the angular

gyrus was subsequently destroyed, with the effect of causing blindness of the right eye.

On post-mortem examination next day the lesion was found to occupy the motor regions specified and the angular gyrus, the rest of the brain and the basal ganglia being intact (fig. 112).

In this case the paralysis was confined to the same movements as result from electric stimulation of the centres specified. In the following experiment the extent of the lesion was still further circumscribed, and the effect, as regards voluntary motion, correspondingly limited.

The left hemisphere of a monkey was exposed in the region of the ascending frontal convolution sufficiently to display (6) (fig. 113), the centre of bicipital action, or supination and

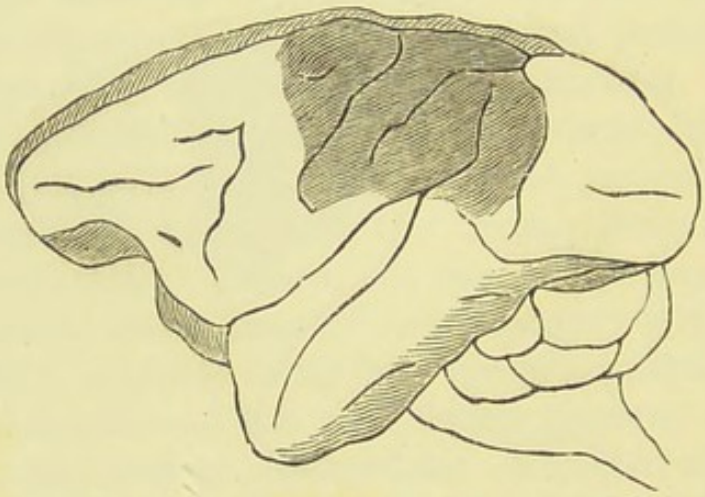


FIG. 112.—Lesion of the Left Hemisphere, causing motor paralysis of the right leg and right hand and wrist, and of some of the movements of the right arm, and loss of sight in the right eye. (Roy. Soc.)

flexion of the forearm. The exact spot being determined by the application of the electrodes, it was then accurately cauterised, just sufficiently to destroy the cortical grey matter. This operation immediately manifested itself in paralysis of the power of flexing the right forearm. All the other movements of the limbs were retained, but when the right arm was placed in an extended position the animal was utterly powerless to flex it, and the limb hung in a state of flaccid extension when the animal was lifted.

It raised things to its mouth with the left hand, the movements of the legs were intact, there was no facial paralysis, and cutaneous and other forms of sensation were unimpaired.

§ 3. In these earlier experiments the duration of the paralytic symptoms consequent on lesion of the motor zone was not determined; but in a subsequent series[1] special attention was directed to this question, as also to the sensibility of the paralysed limbs, and the secondary consequences of the cerebral lesions.

In the first experiment[2] the cortex was destroyed in the middle third of the ascending parietal convolution and adjoining margin of the ascending frontal convolution of the right hemisphere.

The result of this lesion was almost complete paralysis of the left hand, and great weakness of the flexor power of the

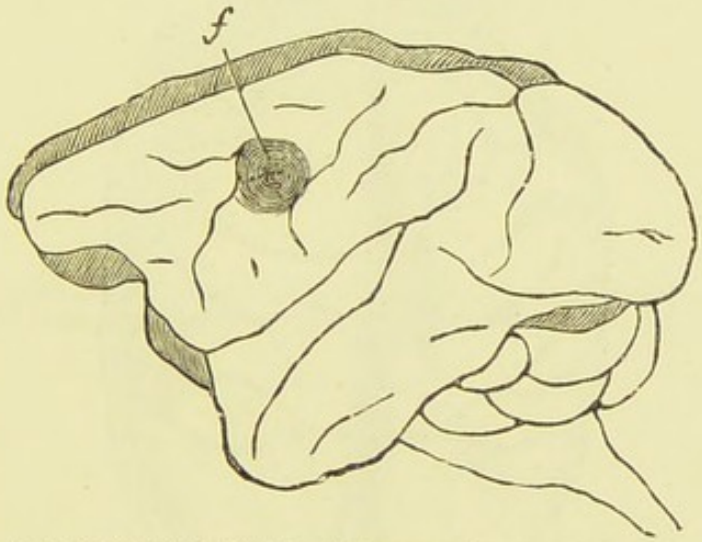


FIG. 113.—Lesion (*f*) of the Left Hemisphere, causing paralysis of the action of the biceps on the right side. (Roy. Soc.)

forearm. The shoulder movements of the limb were unimpaired. The animal could stretch its arm forwards, but could not grip with its hand what it wanted to lay hold of. Tactile sensibility was absolutely unimpaired in the paralysed limb, the slightest touch on it at once exciting the animal's attention, and a painful stimulus, such as a pinch or a touch with a heated wire, exciting as lively signs of sensation as on the other side. The condition remained essentially unchanged for the two months which the animal survived the operation, death occurring from the intense cold of the winter season.

[1] 'The Effects of Lesion of Different Regions of the Cerebral Hemispheres *Philosoph. Trans.* 1884, Part II. (Ferrier and Yeo).

[2] Experiment 15*, *ibid.* fig. 39.

In this case those movements were paralysed which are excited by electrical stimulation of the parts destroyed (see (*a*), (*b*), &c. and (6), (fig. 70), the degree of paralysis being in proportion to the extent of destruction of the respective centres. The lesion was accurately limited, and, owing to antiseptic precautions being employed during the surgical operations, no secondary inflammation, meningitis, or encephalitis was set up.

In the next experiment[1] the cortex was destroyed at the upper extremity of the fissure of Rolando in the left hemi-

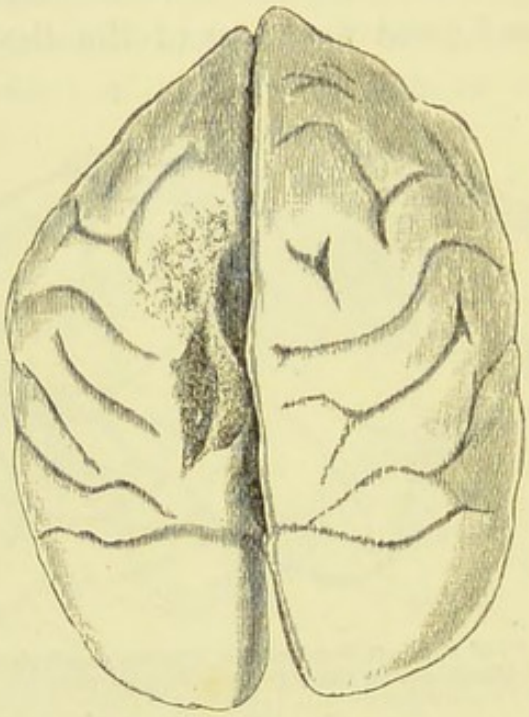


FIG. 114.—Lesion of the Left Hemisphere, causing paralysis of the right leg.

sphere, the lesion invading a considerable extent of the region, irritation of which gives rise to movements of the opposite leg and foot (fig. 70, (1) and (2)). The lesion was purely cortical and did not extend beyond the surface of the medullary fibres, where they radiate into the cortical matter. A slight adhesion of the membranes and erosion of the cortex occurred in advance of the primary lesion, extending into the centre for the forward extension of the arm (fig. 114).

The result of this lesion was dragging of the right leg and almost complete immobility of the foot, while the movements

[1] Experiment 16*, figs. 40-44, *Phil. Trans.* Part II. 1884.

of the thigh on the pelvis were not perceptibly affected. For a few days, owing to the inflammatory adhesion of the membranes over the centre for the forward extension of the arm, there were spasms of the arm at the shoulder. These disappeared, and the arm movements were retained to all appearance intact, but the right leg and foot remained almost completely paralysed. The sensibility of the paralysed parts was in every respect as acute as in the sound limbs, equal reaction being obtained to all the usual tests of cutaneous sen-

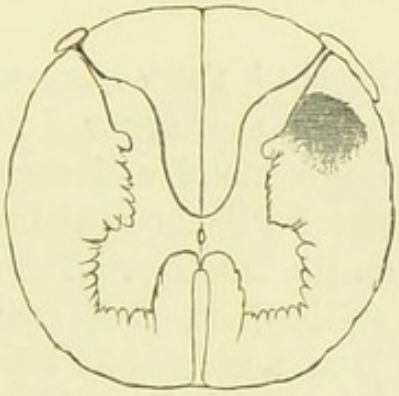


FIG. 115.—Section of the Spinal Cord in the Cervical Region, showing degeneration of the right pyramidal tract consecutive to the lesion seen in fig. 114.

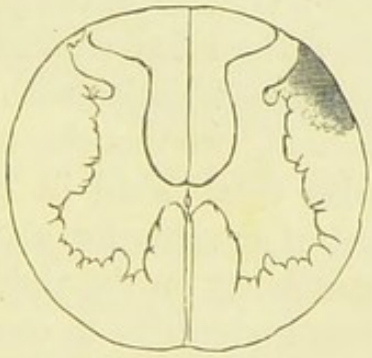


FIG. 116.—Section of the same Spinal Cord in the lumbar region.

sation. Six months after the operation contracture or late rigidity became established in the leg, such as occurs in incurable paralysis in man, with exaggeration of the patellar tendon reaction. The condition remained unchanged at the death of the animal, eight months after the operation.

The cerebral lesion was found accurately limited to the cortex of the upper extremity of the fissure of Rolando. Secondary degeneration was demonstrated by microscopical examination in the medullary fibres of the corona radiata,

and in the pyramidal tracts of the opposite side of the spinal cord as far as the lumbar region, whence emerge the motor nerves of the lower extremity (see figs. 115, 116).

This case proves conclusively that a lesion of the cortex invading the region, electrical irritation of which causes special movements of the opposite extremity, causes permanent paralysis of these movements, and of these alone, and leads to secondary degeneration of those tracts of the internal capsule and spinal cord which connect the cortex with the spinal segment or segments from which spring the motor nerves of the part.

In a third experiment[1] the cortex was extensively destroyed in the region of the upper half of the fissure of Rolando—i.e. ascending parietal and ascending frontal convolutions—of the right hemisphere, the region for the movements of the limbs on the left side. The effect of this lesion was incomplete paralysis of the left arm and leg, the face being unaffected. From immediately after the operation till the death of the animal, nineteen months subsequently, motion was greatly impaired, while sensation was absolutely unimpaired in the left limbs; and, as in the preceding case, in the course of a few months well-marked contracture, or late rigidity, supervened in the paralysed limbs, with exaggerated tendon reactions. In this animal, two months after the first operation, a lesion was also established in the left hippocampal region, with the effect of causing for a time marked impairment of cutaneous sensibility on the right side, without affection of motion. It was instructive to compare the reaction of the paralysed and non-paralysed limbs to tactile stimulation. Whereas in the limbs paralysed as to motion the signs of sensation were active and vigorous, in the non-paralysed limbs various forms of stimulation failed to elicit any signs of perception, or, if so, in a much less degree.

Microscopical investigation after death revealed well-marked atrophy and degeneration of the pyramidal tracts of the right crus cerebri, right side of the pons, right pyramid, and of the left pyramidal or postero-lateral column of the spinal cord as far as the lumbar region.[2]

[1] Experiment 17*, figs. 45–51, *Phil. Trans.* Part II. 1884.

[2] See figs. 45–51, *op. cit.*

In a fourth experiment [1] the cortex was destroyed in the left hemisphere over an area embracing the ascending frontal and ascending parietal convolutions except at their upper and lower extremities, and also the base of the superior frontal convolution. The lesion also trenched somewhat on the anterior limb of the angular gyrus and supramarginal lobule. There was thus destroyed nearly the whole of the motor area on the convex aspect of the hemisphere, the centres for the leg and foot being only partially invaded, and those for the angle of the mouth and tongue almost entirely escaping (fig. 117).

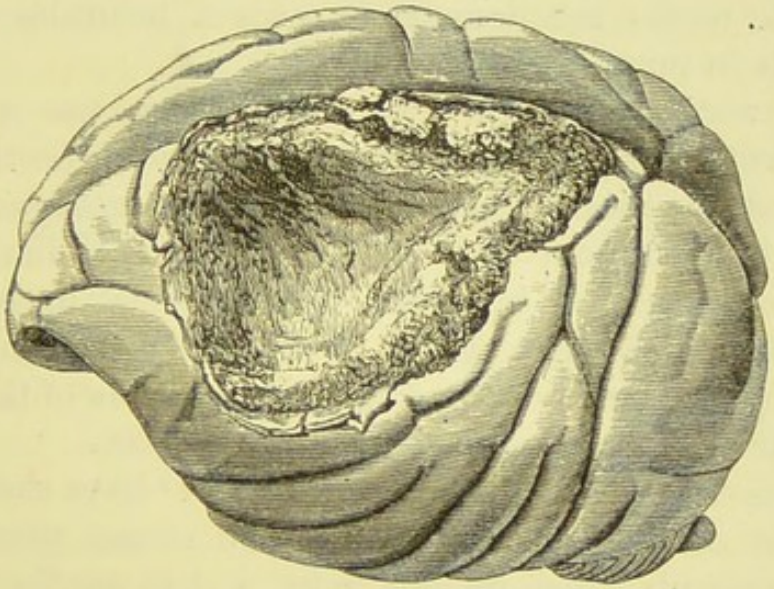


FIG. 117.—Lesion of the Left Hemisphere, causing right hemiplegia.

The result of this lesion was almost complete right hemiplegia with conjugate deviation of the head and eyes to the left side. As in similar cases in man the deviation of the head and eyes was only of comparatively short duration, and the partial facial paralysis at first perceptible also disappeared within a fortnight. But the paralysed condition of the limbs continued very marked. With the exception of slight power of flexion of the thigh and leg the right lower extremity was helpless, and the right arm was utterly incapable of any independent volitional movement. Occasionally, when the animal struggled, associated movements were observed in the right hand, similar to those initiated by the left, but only under

[1] Experiment 18*, figs. 52–55.

such circumstances. The power of prehension was entirely annihilated. Cutaneous sensibility was unimpaired throughout, the slightest touch exciting attention, and a pinch or other painful stimulus causing reaction and signs of sensation quite as vigorous as on the other side.

This animal was exhibited before the Physiological Section of the International Medical Congress in London in 1881,[1] eight months after the operation, when the fact of the right hemiplegia was seen and admitted by all the assembled physiologists. At this time well-marked rigidity or contracture had become established in the paralysed limbs with exaggeration of the tendon reactions, as in cases of incurable cerebral hemiplegia in man.

The investigation of the brain of this animal was entrusted to a committee appointed by the Physiological Section, and the facts of the position of the lesion in the motor zone, and its limitation to the cortex and subjacent medullary fibres, were definitely proved by them. Microscopical investigation also demonstrated the existence of secondary degeneration or sclerosis in the pyramidal tracts of the right side of the spinal cord as far as the lumbar region (figs. 118–120).

The experiments of Horsley and Schäfer[2] have shown that extirpation of the marginal convolution causes paralysis of those movements which remain more or less unaffected after destruction of the centres on the convex aspect of the hemisphere, viz. the movements of the trunk, and those of the limbs on the trunk, effected by the shoulder and hip muscles. In order, however, that these movements should be entirely paralysed it is necessary that the marginal convolution should be destroyed in both hemispheres, as it would seem that the trunk movements are so bilaterally co-ordinated in each marginal convolution that the removal of one alone is not sufficient to cause any very marked effect. When both are removed, however, the most absolute paralysis of the trunk muscles is induced, and the animals remain prone and utterly unable to raise themselves on their limbs.

It is unnecessary to multiply further proofs of the fact

[1] *Trans. Int. Med. Congress*, 1881, vol. i. p. 257.

[2] *Brit. Med. Journ.*, 1884, vol. ii. p. 735.

that in monkeys distinct and permanent paralysis of voluntary motion is induced by destruction of those regions of the cortex, electrical irritation of which gives rise to definite and predictable movements of the opposite side of the body. The paralysis varies in degree with the extent, and is strictly

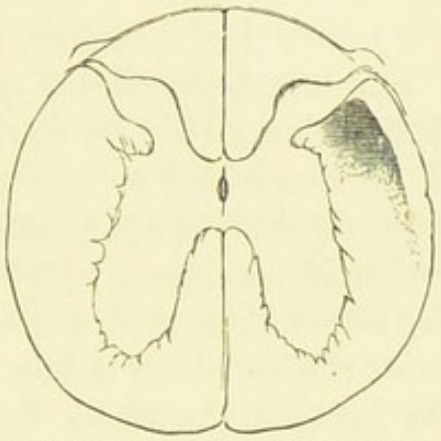


FIG. 118.—Section of the Spinal Cord in the cervical region, showing degeneration of the right pyramidal tract consecutive to the lesion in fig. 115.

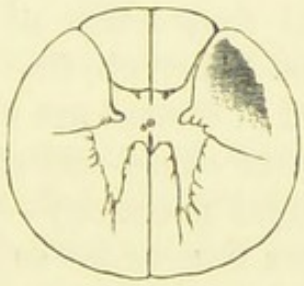


FIG. 119.—Section of the same Cord in the dorsal region.

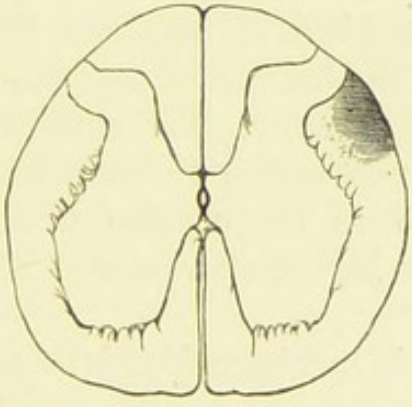


FIG. 120.—Section of the same Cord in the upper lumbar region.

limited according to the position of the lesion. The paralysis affects only that movement or those movements which are thrown into action by irritation of the centre, which is the seat of the lesion. The paralysis is purely motor, sensation

being absolutely unimpaired; and degeneration ensues in those tracts which are developed in relation with the motor centres, and maintain their nutritive integrity through them.

§ 4. The facts of experiment on monkeys as above described have been abundantly confirmed by clinical and pathological researches in reference to the effects of cortical lesions in man. Within the last ten years clinical research, guided by experimental physiology, has accumulated an enormous mass of evidence, which is daily being added to, showing that cortical lesions in the region corresponding to the motor zone of the simian brain, as above defined, cause paralysis of voluntary motion without affection of sensation, which varies in degree with the extent of the destruction, and is limited according to the particular region or centre which is implicated.[1]

If the destruction invades the whole depth of the cortex the paralysis is of an incurable type, and is accompanied by descending degeneration or sclerosis of the pyramidal tracts of the spinal cord, and contracture of the paralysed limbs, precisely as in monkeys. Though the conditions of nature's experiments in the form of disease are not such as are favourable to the elimination of cause and effect—hence the long-enduring chaos of cerebral pathology—yet a careful collation and analysis of instances free, as far as possible, from complications and general cerebral disturbances, have indicated a remarkable concordance between the position of the respective motor centres in the brain of man and those determined by exact experiment in the brain of monkeys.

Of themselves, however, the clinical facts at present accumulated would not suffice to establish more than a probability; but, taken in conjunction with the experimental data, they attain the higher character of sound and stable inductions.

Crural monoplegia has been found associated with limited

[1] See the author's *Localisation of Cerebral Disease*, 1878; Charcot and Pitres, *Revue Mensuelle*, 1877, 1878; and *Revue de Médecine*, 1883; Grasset, *De la Localisation dans les Maladies Cérébrales*, 1878; De Boyer, *Sur les Lésions Corticales*, 1879; Nothnagel, *Topische Diagnostik der Gehirnkrankheiten*, 1879; Exner, *Localisation der Functionen in der Grosshirnrinde des Menschen*, 1881.

lesion at the upper extremity of the fissure of Rolando and paracentral lobule; brachial monoplegia with lesion of the middle of the ascending frontal and ascending parietal convolutions; brachio-crural paralysis with lesion of the upper third of the ascending convolutions; brachio-facial paralysis with lesion of the middle and lower third of the same convolutions; and oro-lingual paralysis or paresis with lesion of the lower extremity of the ascending frontal and parietal convolutions. When the last-mentioned lesion occurs on the left side there is also, with few exceptions, aphasia; and when, as occasionally has happened, the lesion occurs symmetrically in both hemispheres, there is not only aphasia, but complete paralysis of all the volitional movements of the tongue and lips concerned in articulation.[1] This is in accordance with the fact that electrical irritation of the mouth or speech centre (fig. 70 (9) and (10)) induces action on both sides, and hence in order to cause complete paralysis it is necessary that both centres should be destroyed. The same law obtains in respect of the trunk muscles and other bilaterally associated movements.

There is not on record[2] a single unequivocal case of destruction involving the motor zone unaccompanied by paralysis of greater or less extent or limitation; while, on the other hand, there is not another region of the brain which has not been the subject of destructive lesion, times without mention, without any motor paralysis whatever.

§ 5. What is true of the cortex obtains also of the subjacent medullary fibres of the corona radiata. Lesions of the pyramidal tracts of the motor zone which converge to the knee and anterior two-thirds of the posterior division of the internal capsule (fig. 25, *i c*) invariably cause motor paralysis of the opposite side; and it has been found that just as stimulation of the respective cones of medullary fibres gives rise to the same movements as stimulation of the cortical

[1] See an important case of this kind reported by Barlow (*Brit. Med. Journ.* July 28, 1887, p. 103).

[2] See on this the excellent tabular and graphic analysis in Exner's work *Localisation der Functionen in der Grosshirnrinde des Menschen*, 1881; also Charcot and Pitres 'Localisations Motrices,' *Revue de Médecine*, 1883.

centres themselves (Chapter VII. § 5), so destructive lesions cause limited paralysis or monoplegia similarly defined.[1] The differentiation of the pyramidal tracts has further been demonstrated[2] by the fact that the area of secondary degeneration in the internal capsule and foot of the crus cerebri varies according to the portion of the cortex which has been destroyed. Apart from the anterior division of the internal capsule, which as will be seen (§ 25) degenerates in relation with lesions of the prefrontal lobe, the tracts forming the knee and anterior two-thirds of the posterior division are in relation respectively from before backwards with the oro-lingual, facial, brachial, crural, and trunk muscles. Thus destruction of the mouth-centres causes degeneration of the fibres forming the knee of the internal capsule; those of the middle of the ascending convolutions, the fibres posterior to the knee; and those of the upper extremity of the ascending and marginal convolutions, of the fibres which form the posterior third of the motor division of the internal capsule. These fibres maintain their relative position in the foot of the crus; the innermost, or those nearest the median line, corresponding to those in relation with the prefrontal lobes; and the outermost, or those which lie immediately in relation with the sensory tracts of the outer third or of the crus, being in relation with the cortical centres situated at the upper extremity of the fissure of Rolando and paracental lobule.

§ 6. When, however, we turn from man and the monkey to the animals lower in the scale, such as the cat, the dog, and the rabbit, we meet with facts which to some appear opposed to the doctrine abundantly illustrated by the foregoing experiments, that there are special motor centres in the cortex cerebri. Much controversy has taken place on this topic, and owing mainly to a narrowness of view and neglect of comparative physiology, doctrines have been propounded which, however well according with the results of experiment on one

[1] Pitres, *Lésions du Centre Ovale*, 1877; Hughes Bennett, 'Case of Brachial Monoplegia,' *Brain*, April 1885.

[2] Brissaud, *Contraction Permanente des Hémiplégiques*, 1880; see also Horsley, 'On Substitution in Reference to Cerebral Localisation,' *Lancet*, July 5, 1884.

order of animals, are altogether at variance with those on animals higher in the scale. It is, however, inconceivable that brains constructed on the same anatomical type should differ fundamentally in their physiological organisation, and we may assume as certain that, however much the facts of experiment on the motor centres of dogs and rabbits may appear opposed to those of monkeys, they are not so in reality, but are capable of being embraced with them in one comprehensive and harmonious generalisation.

§ 7. The centres for the movements of the limbs in dogs are, as indicated by the electrical reactions, situated in and around the crucial sulcus. When this region is destroyed in the one hemisphere the movements of the opposite limbs are at once affected in a very striking manner.[1]

At first this appears to be absolute paralysis, so that the limbs are powerless to support the animal's weight, and double up under it. Shortly, however, frequently within a few hours, considerable improvement occurs, so that the animal can stand somewhat insecurely, and make attempts to walk. In doing so it generally turns in a circle towards the side of lesion. The limbs, especially the fore limb, tend to double up, and the foot is planted awkwardly, resting frequently on the dorsal instead of on the plantar surface, and the hind leg is dragged, instead of being lifted clear from the ground in the usual manner. Walking, at first impossible, is soon attempted, the animal tending to fall, and frequently actually falling over on the side, especially if the movements are at all hurried. Gradually, however, the power and control of the limbs are regained to such an extent that the animal can stand and walk without exhibiting any very noteworthy abnormality on cursory inspection. All this may occur within a few days after the operation. But, though it can stand and walk and run, it still continues for a long time very unsteady, and the limbs tend to slip and diverge outwards if the floor is smooth or if the animal turns round quickly. Even this may become less pronounced after the lapse of months, but no animal ever

[1] Hitzig, *Untersuch ü. das Gehirn*, 1874; Carville and Duret, *Sur les Fonctions des Hémisphères Cérébraux*, 1875; Goltz, *Ueber die Verrichtungen des Grosshirns*, 1881.

entirely recovers;[1] and, as Tripier[2] has ingeniously shown, the paretic condition of the limbs can always be rendered apparent and intensified by the administration of a dose of morphia, or by conditions causing general prostration of the nerve centres.

In the cat the phenomena following destruction of the motor centres are essentially the same as in the dog. In the case of the rabbit the effects are less marked and still more transitory.

§ 8. There is thus a very remarkable difference between the monkey and the dog in respect to the degree and duration of the powerlessness of the limbs after destruction of the cortical centres, and the question is, how are these differences to be explained on the hypothesis that the cortical centres in these animals are constructed on the same type, and perform homologous functions?

The affection with which we have to deal, as will be discussed more at length subsequently, is in both cases a purely motor one, and the centres or regions in question are strictly motor, but motor in a special or limited sense, viz. psychomotor, or concerned in the execution of consciously discriminated or volitional movements proper. The differences observable as to the effects of destruction of the cortical centres in different animals depend on the degree or extent in which conscious discrimination, as distinct from automaticity or mere reflex action, is concerned in the ordinary modes of activity manifested by the animals operated on. In order properly to appreciate these differences, it is necessary to revert to certain facts already alluded to in a former chapter (Chapter IV.)

It has been shown that entire removal of the cerebral hemispheres operates differently in different classes or orders of animals, in so far as relates to their motor stability and powers of response to external stimulation. In the fish, frog, and pigeon the removal of the hemispheres exercises little or no appreciable effect on the faculties of station and locomotion. Under the influence of stimulation from without these animals swim, jump, or fly with as much vigour, apparently, and

[1] Obersteiner, 'Die Motorischen Leistungen der Grosshirnrinde,' *Med. Jahrb.*, Heft II. 1878.

[2] *Revue Mensuelle*, Sept. 1877, and Jan. 1880.

precision as before. In the rabbit the destruction of the hemispheres, while greatly impairing the motility of the fore-limbs, does not render equilibration impossible, or destroy the power of co-ordinated movements of locomotion in response to appropriate external stimuli.

In the dog, however, the removal of the hemispheres renders the animal completely prostrate and unable to stand or walk. Whether its powers might be regained, to some extent at least, in course of time is probable, but difficult to determine experimentally, on account of the fatality of the necessary operations.

§ 9. The independent organisation of the lower centres is thus seen to vary according as we ascend or descend the animal scale.

In proportion to the variety and complexity of the forms of motor activity of which the animal is ultimately capable, the longer the period necessary for the acquisition of volitional control over the limbs. Many of the lower animals start from birth with all their powers of movement already fully organised and capable of being exercised; in most the period of helpless infancy is extremely short, as compared with that of the simian or human young. In these every exact movement is the result of a long and laborious process of education, even though this is rendered comparatively easy by the previous work of the race inherited in their nerve centres.

The more machine-like or automatic the movements are at birth, the less the disturbance created by the destruction of the centres concerned in volitional action. Hence in the fish, frog, and pigeon the removal of the cortical centres has comparatively little effect on the motor powers ordinarily exhibited.

Where voluntary control is speedily acquired, or automaticity inherited or rapidly established, as in the rabbit and dog, the centres of voluntary motor acquisition may be removed without completely or permanently interfering with the powers of locomotion. Locomotion is still possible through the agency of the lower centres, in which this mode of activity is mechanically organised, and may be set in action in response to various forms of external or internal impulse. The more the move-

ments are dependent on conscious discrimination and volitional impulse, the more marked and enduring is the paralysis resulting from lesion of the centres of volitional action and registration. Hence the complete and lasting character of the paralysis is consequent on destruction of the cortical motor centres in man and the monkey.

The experiments of Soltmann[1] on young dogs indicate that at birth the cortical motor centres are not fully developed, and do not respond to electrical stimulation before the tenth day of extra-uterine life. In accordance with these facts he has found that extirpation of the cortical centres before the tenth day causes no perceptible disturbance of the motor powers, such as invariably ensues when the animal has reached a more mature age. The first centres to respond are those for the forelimb, and it is precisely the movements of the forelimb which are most affected by lesion of the motor zone. Up to the tenth day all the movements of the puppy are mere reflex or automatic, and such as are primarily organised in the lower centres. These are unaffected by removal of the centres of volitional control and acquisition, and it is only when true volition becomes established that destruction of the cortical centres produces the characteristic disorders of movement which have been described.

And as volition enters more especially into the motor activities of the forelimb, so the forelimb is relatively more affected than the others. The degree of development and control over the movements which a puppy reaches in ten days or a fortnight are not attained by the human infant under a year or more; so that if we were to estimate the degree of paralysis resulting from the destruction of the cortical centres simply by the length of time required to reach the same standard of development, it would be at least thirty times more marked in man than in the dog.

§ 10. Besides these differences in the primary organisation of the nerve centres in different animals, there are certain facts relating to associated and bilateral movements which have an important bearing on the question under considera-

[1] 'Experiment. Stud. ü. d. Funct. d. Grosshirns d. Neugebornen,' *Jahrb. f. Kinderheilkunde*, Bd. ix. 1876.

tion. In hemiplegia or unilateral paralysis of motion from disease of the opposite hemisphere, it is found in man that the individual movements are not all equally affected, and that in the process of recovery some are regained before the others. Thus it is found that when the arm and hand are perfectly powerless some degree of volitional control over the leg and foot may still be retained. The facial muscles are never entirely paralysed, and in particular the orbicularis oculi remains almost unaffected, so that the eye on the paralysed side can be closed almost as well as the other. In this there is a marked contrast between cerebral facial paralysis and peripheral facial paralysis, depending on direct lesion of the seventh cranial nerve. In the latter case the orbicularis oculi is absolutely paralysed, so that the eye cannot be closed.

Generalising from these facts, it may be said that the more independent movements are most affected, while such as are usually associated in action with those of the opposite side—the eyelids and other facial muscles, and many of the leg muscles—are less paralysed and more speedily recover. The varied and delicate movements of the hand are most of all impaired, and are the last to be re-established.

The limbs of quadrupeds are, as regards the general character of their movements, more like the lower than the upper limbs of man, inasmuch as they are capable of comparatively few independent movements, and, as a general rule, are exercised only in alternating or associated action with each other. This fact of bilateral association, added to the greater degree of automaticity in the movements of the lower vertebrates, serves still further to explain the differences between them and the higher animals in respect to the effects of cortical lesions. Some movements are bilaterally represented in each hemisphere, and are thrown into action conjointly by electrical irritation of the cortex. This holds especially of the oro-lingual and trunk movements. Others which are not bilaterally represented in the cortex directly may be, as Broadbent has suggested, so connected by commissural fibres in the lower centres that both may be thrown into action by an impulse initiated by the one hemisphere. That this is the case is supported by many facts. Though moderate irritation of the

cortex produces movements of the limbs only on the opposite side, yet under severer irritation, such as gives rise to epileptiform convulsions, all four limbs may be thrown into action. In hemiplegia also strong energising of the sound hemisphere is apt to act also to some extent on the paralysed side. In one of the experiments above related (p. 355) I noted the fact that frequently when the animal used its left hand powerfully the right hand also, otherwise absolutely powerless, tended to close firmly; and often when scratching movements were made with the left hand the right also scratched purposelessly in mid-air, and sometimes continued to do so for a distinct interval after the other had ceased. A hemiplegic patient when asked to move his paralysed leg is absolutely unable to do so; but if he is asked first to move the sound leg, and then to try with the paralysed one, he may frequently succeed in moving it with a considerable degree of power. But commissural connections between the corresponding spinal nuclei on the two sides would not, as Horsley[1] has pertinently remarked, ensure the associated action of the limbs in locomotion, inasmuch as in locomotion the fore leg and the hind leg act together, and when one leg is flexed the other is extended. But we are not limited to mere commissural fibres between the corresponding spinal nuclei in endeavouring to explain bilateral association. Without anatomical commissural connections movements may be so constantly functionally associated with each other, that the initiation of the movement on the one side may call the other into play. The movement need not be the same on the two sides. The closest functional associate of the fore leg in quadrupeds is the opposite hind leg, and, as we have already seen, since in the lower animals the movements concerned in locomotion are organised in the mesencephalic and spinal centres, there seems little difficulty in understanding how the centres of locomotion may be thrown into action bilaterally by an impulse proceeding from the one hemisphere alone.

There is reason to believe that the initiating impulse of the sound hemisphere is capable of compensating in large measure for the loss of the centres in the other by the development of

[1] 'On Substitution, &c.' *Lancet*, July 5, 1884.

freer channels of communication between the bilaterally associated lower centres. An interesting experiment confirmatory of this hypothesis has been described by Soltmann. The motor area of the left hemisphere was destroyed in a puppy of four or five days old. No perceptible disorder of movement could be discovered either immediately or some days after the operation. The wound healed, and at the end of eight weeks the animal was perfectly well, though small. At the end of three months the motor zone of the right hemisphere was exposed and stimulated by the electric current, when it was seen that irritation of the centre for the left foreleg caused also similar movement of the right. Isolated action of the left leg could never be obtained, but always the conjoint action of the two.

§ 11. But though from these and other facts it is clear that the sound hemisphere is capable of influencing in greater or less degree the movements of the limbs, and other parts, on both sides of the body, it is impossible to explain the comparatively slight impairment of the ordinary motor activities of the dog on destruction of the cortical centres in the one hemisphere merely by the compensatory action of the other. If it were only a matter of compensation by the cortical centres of the other hemisphere, it ought to follow that destruction of these also should cause complete paralysis on both sides. This, however, is not the case. Carville and Duret[1] destroyed the motor centres of the limbs in the right hemisphere in a dog. This was followed by the usual paralysis, at first, as usual, very pronounced, but at the end of from six to eight days apparently recovered from. The left hemisphere was then similarly operated on, with the result of causing paralysis of the right limbs of the usual type, without reinducing the paralysis of the left side. But what seems still more remarkable, and apparently inconsistent with the specific localisation of motor centres in the cortex, is the fact that even after destruction of the motor centres in both hemispheres spontaneous and intentioned movements of considerable complexity are still capable of being carried out. When

[1] 'Fonctions des Hémisphères Cérébraux,' *Archives de Physiologie*, 2e Série, tome i. 1875.

the operation is performed on puppies it would appear, from a successful experiment of this kind related by Soltmann, that, beyond general retardation of development, no special defect as regards motor power is observable. In adult animals, on the other hand, though immediately after extensive bilateral lesion [1] there is a condition of general powerlessness, yet this improves to a considerable extent, and station and locomotion, though awkward and unstable, become ultimately possible. But the animals never entirely recover, and the forepaws especially are never capable of being employed for any independent movements.

§ 12. It has been assumed by Carville and Duret, and others, that this apparent recovery of volitional control over the limbs, which, however, is more apparent than real, justifies the hypothesis of Flourens and his followers that a process of compensation is effected by other parts of the hemispheres taking up and performing the functions of the centres which have been destroyed. If this hypothesis had any real foundation, however, it ought to apply to monkeys and man. But this is not the case, for the paralysis resulting from destruction of the motor centres in these animals is permanent, and resembles in all its characters incurable cerebral paralysis in man.

It is a hypothesis, moreover, altogether inconsistent with the theory of specific localisation of function. If we were to suppose it possible that the functions of the leg centres could be taken up by the neighbouring occipito-angular region, we should have the very remarkable substitution of a motor by a sensory centre; a region which is at one time a centre of

[1] It is questionable whether any experimenter has ever entirely destroyed the whole of the motor area in both hemispheres. In the dog exhibited by Professor Goltz at the International Medical Congress in London, 1881 (see *Trans. Int. Med. Congress*, 1881, vol. i. p. 218 *et seq.*) a considerable portion and of the motor centres of the limbs was perfectly intact in both hemispheres, especially in the left (see figs. 14*a* and 15*a*, and reports by Klein and Langley, pp. 242*a* and 242*b*. See also the further description of the right hemisphere by Langley in the *Journal of Physiology*, vol. iv. p. 292, and figures 1–3). Yet in this animal, retaining so much of the centres for the limbs, there was observable an extraordinary awkwardness of movement. Its legs tended constantly to slip and give way, and, as Goltz remarked, it was unable to use its paws to hold a bone when gnawing it, as dogs ordinarily do.

visual perception, becoming a centre of voluntary motion, or even a sensory and motor centre at one and the same time, if there is no break in the continuity of function. Such a mode of interpretation is no more justifiable than the supposition that the organ of vision may take up the functions of the organ of hearing, or that a nerve may be at one time a motor nerve, and at another a sensory nerve, or perform both functions at once. For the specific localisation of function depends not on accident or indifferentism, but upon structural differences and connections which render each region as distinct from another as the eye from the ear, or the leg from the tongue. The occipito-angular region is the cortical expansion of the optic tract in the same sense as the retina in its peripheral expansion, and destruction of either expansion leads to atrophy of the optic nerves. The cortical motor region is the cerebral origin of the pyramidal tracts, and destruction of this region, and of none other, leads to degeneration of the pyramidal tracts; and not only so in general, but each cortical centre is in relation with its own particular bundle of pyramidal fibres, and none other, so that limited destruction of the motor zone causes limited degeneration only of those fibres of the pyramidal tracts which are structurally related to the centre in question. The foundation of cerebral localisation resting, as is proved by such facts, on anatomical differences and connections, we may dismiss the hypothesis of substitution of one part by another as involving a contradiction in terms. It is necessary, therefore, to seek for some other explanation of the apparent retention of voluntary motor power in dogs after removal of the cortical motor centres, consistent with the doctrine of specific localisation so amply demonstrated by the facts of experiment and clinical research in monkeys and man. For it is not to be supposed that animals constructed on the same anatomical type should differ so fundamentally in their cerebral organisation that specific localisation of function should be true of one and absolutely false in respect of another. Though dogs appear to recover from the effects of destruction of the cortical motor centres the recovery is found, on careful examination, to be more apparent than real. As a matter of fact, they never recover those movements which are essentially cortical,

nor do dogs which have been deprived of their cortical centres at birth ever acquire them. Though a dog after destruction of its cortical motor centres is able to stand, and walk, and run, it never, even at best, performs these actions as well as the fish, frog, or pigeon without any cerebral hemispheres at all. It is obvious that for these modes of activity the cerebral hemispheres are not absolutely indispensable. The independent organisation in the lower centres of all the adjustments involved in station and the movements of translation, appears to be complete and perfect in the lower vertebrates, such as the fish, frog, and pigeon; but in the higher animals the co-operation of the centres of voluntary motion and registration is necessary, and this in varying degree. In proportion to the extent to which conscious discrimination is involved in the modes of activity displayed by the animal appears to be the time necessary for their acquisition, and in the same proportion are they impaired by destruction of the cortical motor centres. This reaches its extreme in man in whom the motor capabilities are most complex and varied, and in whom the longest education and experience are necessary to develop and establish complete and perfect control over the limbs. In dogs less education is required, and the effects of destruction of the cortical motor centres are much less obvious; but even in them the mesencephalic and lower centres never attain the same perfection of independent organisation seen in the fish, frog, and pigeon. In order that a dog may be capable of exhibiting a degree of responsive reaction similar to that of a pigeon deprived of its hemispheres, it is necessary that the basal ganglia—the corpora striata and optic thalami—should remain uninjured; and even in such case the reactions and manifestations are greatly wanting in stability and precision. The so-called recovery which occurs in dogs after destruction of the cortical motor centres extends only to the brute force of the limbs, and to such movements or muscular combinations as are primarily or secondarily organised in the lower centres, and require no conscious discrimination for their accurate performance. Even these are permanently unstable and awkward, and capable of being effected only under favourable conditions. Equilibrium is easily overthrown, the limbs

slip and double up on a smooth floor, or trip up over comparatively slight obstacles or inequalities, and are incapable of that quick adaptation which characterises a normal animal under similar conditions. For all purposive actions implying conscious discrimination the limbs are permanently paralysed. The dog can never use its paw as a hand.[1] It cannot use the limb to dress its coat, or reach it forth to seize a piece of food lying just beyond its muzzle like a normal dog when tied up. It cannot fix or steady a bone which it wishes to gnaw, or clasp the female in sexual embrace. If it has learnt to 'give a paw' at the word of command, it looks distressed and sorrowful, and fails to comply with the order.[2] In respect of these and all actions and tricks in which the limb is employed as an instrument of volitional purpose, the dog remains permanently incapacitated.

There is, however, a great difference between the dog deprived of its cortical motor centres and a pigeon deprived of its cerebral hemispheres. The latter is a living mechanism acting only in immediate response to appropriate external stimuli; whereas the dog retains spontaneity, and exhibits a manifold variety of activity under the same external conditions. But a dog, deprived only of its cortical motor centres, retains its sensory centres, and is therefore capable of sensation, ideation, and emotion. It is not dependent for its activity on immediate impressions on its organs of sense, but has within itself the springs of action in the mediate form of revived or ideal impressions and emotional states. There is, however, no essential difference as regards causation between actions conditioned by present impressions on the sensory organs and those conditioned by revived or ideal impressions, for the same apparatus is concerned in both. Under the influence of ideational or emotional states, the sequence and causation of which may not be apparent, the dog may walk, run, or give expression to its desires in a manner indistinguishable from ordinary volition. Only those actions are possible,

[1] Goltz, *op. cit.* p. 30.

[2] Goltz says that one or two of his animals have again learnt to 'give a paw,' others not. It may be confidently asserted that the cases of recovery were cases of incomplete destruction of the cortical centres in the first instance.

however, which are primarily or secondarily automatic and organised in the lower centres. All actions not so organised, and still dependent on conscious discrimination and the exercise of attentive volition, are effectually and permanently annihilated.

§ 13. Views have been propounded by other authors with respect to the functions and significance of the cortical motor centres, which appear to me neither justified by the facts of experiment on animals, nor consistent with those of clinical observation in man.

Schiff[1] maintains that the movements resulting from irritation of the cortex are of a reflex nature, and that the affection of motility following destruction of the cortical centres is essentially only an ataxy, dependent on loss of tactile sensibility, and exactly of the same nature as that resulting from section of the posterior columns of the spinal cord.

In support of this he argues that those agents which annihilate reflex excitability also annihilate the electrical excitability of the cortex. This is true, but the excitability of the cortex does not follow the same laws as those regulating merely reflex actions. Reflex actions are still readily excitable under conditions which entirely annul the excitability of the cortical centres. Schiff ascribes the movements resulting from electric stimulation to irritation of the fibres of the posterior columns, which—altogether without proof and contrary to all recent anatomical investigations—he assumes approach the cortex before turning downwards to reach their true centres at the base. In order to account for the secondary degeneration which ensues in the pyramidal tracts after destruction of the cortex, he further assumes that the pyramidal tracts, issuing from the basal centres, ascend near to the surface before turning downwards to pursue their path in the crura cerebri and lateral spinal tracts. The cortex itself, according to this imaginary anatomy, would appear to be altogether indifferent material, merely forming a covering for fibres which come near it, but form no connection with it.

The resemblance which Schiff traces between the effects of

[1] *Archiv für Experiment. Pathol. u. Pharmacol.*, Bd. iii. 1874; Pflüger's *Archiv f. Physiologie*, Bd. xxx. 1883.

destruction of the cortical motor centres and the ataxy following section of the posterior columns of the spinal cord is of the most flimsy and superficial character, and disappears entirely on more careful investigation. The term ataxy is altogether inapplicable to the symptoms observed in man and monkeys on destruction of the cortical centres. In these there is a true motor paralysis varying in degree, as has been seen, according to the volitional independence of the movements affected. In dogs and other quadrupeds there is less general powerlessness, but those movements are most affected which are least so in ordinary ataxy. It is the independent and volitional movements of the limbs, such as the use of the paw as a hand, which are paralysed in dogs; while associated movements of the limbs, such as are concerned in running, leaping, &c. which are most affected in ataxy, are least impaired after destruction of the cortex. The movements are more or less insecure, but this is attributable to motor weakness in general, and not to any ataxic disorder.

Schiff, in further support of his theory of the identity between the effects of section of the posterior columns and destruction of the cortex, makes the extraordinary statement that after section of the posterior column on one side the motor area of the opposite hemisphere ceases to be excitable after the lapse of about four days. This he regards as a proof of the continuity of the posterior column with the parts which ordinarily react to the electrical stimulus. He assumes that the section of the posterior column, by severing it from its nutritive centres in the posterior spinal ganglia, leads to ascending degeneration as far as the cortex, so that the fibres are no longer capable of being excited and giving rise to reflex reactions.

It is true, as Schiff states, that the operation for section of the posterior column as he performs it leads to abolition of all reactions from the cortex in the parts situated below the section, but the explanation is a very different one from that which he gives. There is no degeneration up to the cortex, but, as Horsley[1] has satisfactorily demonstrated, the pyra-

[1] Horsley, 'On the Relation between the Posterior Columns of the Spinal Cord and the Excito-motor Area of the Cortex, &c.,' *Brain*, April 1886.

midal tract, injured by the operation for section of the posterior column owing to secondary inflammatory changes, undergoes degeneration below the section, so that it ceases to be capable of transmitting motor impulses to the parts with which it is in relation. But this result only ensues when the operation is not carried out in such a manner as to prevent the extension of the primary lesion by secondary inflammation. That the motor area continues excitable, notwithstanding the destruction of the posterior column, even in cases where the lateral column becomes implicated, is shown by the occurrence of the ordinary reactions in the parts deriving their motor supply from the parts above the lesion.

Schiff holds that the posterior columns of the spinal cord are the paths of tactile sensibility or touch proper, as distinct from the other forms of common sensibility, and he attributes the ataxy which results from section or disease of these columns to the loss of tactile sensibility. These questions have already been discussed (Chapter II. § 10), and we have seen reason to regard Schiff's views as to the functions of the posterior columns and as to the cause of ataxy to be entirely erroneous.

§ 14. The assertion made by him, as well as by Tripier,[1] Munk[2] and others, that removal of the cortical motor centres causes loss of tactile sensation has no better foundation.

Munk, indeed, goes farther than Schiff, and holds that not merely tactile sensibility, but common sensibility in general is abolished by lesion of the cortical motor zone. Munk's statements are justly ridiculed by Goltz[3] as being unsupported by any evidence worthy of consideration, and directly contradicted by his own experiments, as well as those of Hitzig, Schiff, and my own.

The conclusion that tactile sensibility is lost or diminished after destruction of the cortical motor area is based on defective methods of investigation and erroneous interpretation of the reactions of the lower animals to sensory stimulation. Though an animal does not react so readily to sensory stimula-

[1] 'De L'Anesthésie produite par les Lésions des Circonvolutions Cérébrales,' *Revue Mensuelle de Médecine et Chirurgie*, 1880.

[2] *Op. cit.*

[3] 'Verrichtungen des Grosshirns,' Pflüger's *Archiv*, Bd. xxxiv. 1884, p. 467.

tion of the paralysed side it does not follow that this is due to diminished or absent perception of the stimulus. An animal may not react, or react less energetically, to a sensory stimulus, not because it does not feel it the less, but because it is unable, or less able, to do so from motor defect. It is astonishing what apathy or indifference some animals display towards certain forms of stimulation, such as gradually increasing pressure on the fingers or toes which one would regard as well calculated to elicit reaction or signs of uneasiness. Unless the stimulus is of a nature to at once excite attention, or to evoke reflex action, it may appear to be altogether unperceived. All that the experiments of Schiff and Tripier demonstrate is that motor reactions are less readily evoked on the side opposite the cortical lesion. But the same thing occurs in cases of purely motor hemiplegia in man.

Cutaneous reflexes are less readily excitable on the paralysed side, though the patients testify to the fact that they feel and localise the tactile stimulus as readily and acutely on the one side as the other.[1]

It is easy by devising methods calculated to evoke signs of true sensation, as distinct from merely reflex reaction, in the lower animals, to prove beyond all question that in them also sensation is entirely unaffected by lesions of the cortical motor zone. In monkeys, attentive to all their surroundings, it is as a rule only necessary to gently touch the paralysed side to elicit the most indubitable signs of attention. In one animal[2] in which for purposes of comparison I established lesion first in the motor area of the right side, and afterwards in the hippocampal region of the left side, there was diminished

[1] Why the reflexes should be diminished in pure motor hemiplegia of cerebral origin is not quite clear. It extends not merely to the reactions of the limbs, but also to the cremasteric and other reflexes which are not obviously under volitional control. When the cord is divided the reflexes are more active. It has been supposed by some that the spinal reflexes are inhibited by the cerebral lesion. It appears to me more probable that it is simply a case of greater or less diffusion of the stimulus. Ordinarily the cerebral centres co-operate with the spinal centres, even in the simplest reflex reactions. When the cerebral centres are destroyed the sensory stimulus is diffused upwards and lost. When the cord is divided the sensory stimulus is concentrated in the spinal centres, and more readily calls forth reflex reaction.

[2] Experiment 17, *Phil. Trans.*, 1884, Part II.

reflex reaction in the left limbs, though the signs of sensation were distinct; whereas on the right side, though the reflex reactions were more readily excitable than on the left, yet the animal bore with perfect indifference stimuli which caused active signs of uneasiness when applied to the paralysed limbs.

Goltz[1] relates an extremely instructive experiment on a dog, which shows in the clearest possible manner that tactile sensibility is absolutely unimpaired on the side opposite the lesion of the cortical motor zone. Taking advantage of the well-known fact that dogs snarl when touched while engaged in eating any choice morsel, he touched the right side of a dog so occupied, which had had its motor region in the left hemisphere destroyed some time previously. The animal responded on every occasion with the characteristic signs of displeasure to the slightest touch.

A similar satisfactory proof of the retention of tactile sensation in a cat after destruction of the opposite cortical motor zone is furnished by Bechterew.[2] It is a familiar observation that a cat dislikes having its feet wet, so that if it should accidentally step on a wet place it will stop and shake its paw dry before proceeding further; or, if while it is indolently slumbering, a drop of water falls on it, it will start up and make off hastily. Or it will close its eyes and contract its ears if its paw is gently touched unobserved. After verifying these facts in a cat about to be operated on, Bechterew removed the cortex in the region of the sigmoid gyrus of the left hemisphere. On recovery from the chloroform narcosis the animal exhibited the characteristic motor disorders of the right limbs, and was unable to use the right paw for any independent volitional act. But touching the ear or the sole of the foot of the right as well as of the left side induced the same closure of the eyes and drawing in of the ears as before; and the sprinkling of a few drops of water on its paralysed side caused the animal to start and make off as before.

In presence of facts such as these it is useless to contend

[1] Pflüger's *Archiv*, Bd. xxxiv. 1884, p. 465.

[2] 'Wie sind die Erscheinungen zu verstehen, die nach Zerstörung des motorischen Rindenfeldes an Thieren auftreten,' Pflüger's *Archiv*, Bd. xxxv. 1885, p. 137.

that tactile sensibility is in any measure impaired by destruction of the cortical motor region.

§ 15. It is unquestionable that in man paralysis associated with lesion of the cortical motor zone is in the vast majority of instances an essentially motor affection, and is unaccompanied by any defect in the domain of sensation, whether tactile, thermal, or otherwise. In old-standing cases, where the limbs have become rigid, cold, and œdematous, sensation may be found more or less obtuse, but not more so than would be naturally expected from the condition of the tissues of the limb so induced. But, apart from this, sensation is keen and to all tests unimpaired in the limb which is utterly beyond the control of the will.

It is, however, true that clinical records furnish instances in which sensation has been abolished or impaired in connection with and, as some contend, apparently due to lesions of the cortical motor area. But it is also true that lesions have been found in certain regions—the prefrontal, occipital, and temporal—without any discoverable symptoms whatever; and on the other hand, as Brown-Séquard[1] has shown, there is scarcely a symptom of cerebral disease that has not been found in connection with lesions situated in these regions, as well as in the brain indiscriminately. These facts, instead of establishing causal relationships, serve only to illustrate the comparative impotence of purely clinical research towards the elucidation of the functions of particular regions. Morbid anatomy is not equivalent to pathology, and less so in the case of the brain than elsewhere. The extent of the part visibly diseased is by no means a measure of the extent or position of the functional or organic derangement that actually exists. If the mere visible anatomical lesion were always to be regarded as the true cause of the symptoms, we might find with Exner a centre for almost every function in the most diverse cerebral regions; or conclude with Brown-Séquard that there is no localisation of function whatever, and that a cerebral lesion, wherever situated, produces symptoms only through some dynamical influence on the true centres situated

[1] 'Lectures on the Physiological Pathology of the Brain,' *Lancet*, 1876 and 1877.

somewhere unknown. Causation is not established unless an invariable and unconditional relationship has been proved to exist between a particular lesion and a particular symptom. In the case of the motor area it has been satisfactorily demonstrated that a destructive lesion invariably gives rise to motor paralysis, local or general, according to the position and extent of the lesion.

That in some instances impairment of sensation has been observed along with paralysis of motion in connection with lesions apparently confined to the cortical motor area does not suffice to establish a causal relationship between the anatomical lesion and the sensory defect; for a single case of destructive lesion of the motor area without anæsthesia is sufficient to overthrow the apparent causal connection founded on a host of positive instances. But as in reality the cases in which anæsthesia has been observed in connection with destructive lesion of the motor area are quite exceptional in comparison with those in which all sensory impairment has been distinctly disproved, it seems almost inconceivable that they should be seriously adduced as good evidence in support of the sensory functions of the motor zone.[1]

Strictly cortical lesions of the motor area do not cause anæsthesia in any form, and it may be laid down as a rule, to which there are no exceptions, that if anæsthesia is found along with motor paralysis, the lesion is not limited to the motor zone, but implicates also organically or functionally the

[1] As a type of the evidence and arguments in favour of the sensory function of the motor zone the reader may refer to a paper by Petrina ('Sensibilitätsstörungen bei Hirnrindenläsionen,' *Zeitsch. f. Heilkunde*, Bd. ii. p. 375, 1881). The author quotes six cases of what he regards as strictly limited cortical lesions associated with sensory disturbances.

In one of these a small hæmorrhagic tubercle, the size of a lentil (!), situated in the right upper parietal lobule, is credited with having been the cause of left hemiplegia and anæsthesia; and in another a small cheesy tubercle, the size of a hemp-seed (!), situated in Broca's convolution, is regarded as the cause of aphasia, paralysis of the right side of the face and arm, and anæsthesia of the right side of the trunk.

That such minute morbid specks, which might well have reached three times the size without causing any appreciable disturbance of the parts in which they were situated, should be regarded as the real cause of the widespread derangement of cerebral functions observed in these two cases is a truly marvellous phenomenon.

sensory tracts of the internal capsule or the centres to which they are distributed (the falciform lobe).

§ 16. Hitzig[1] and Nothnagel[2] attribute the disorders of motility consequent on destruction of the cortical motor zone to loss of the muscular sense, and assimilate the condition to that of ataxy. Hitzig says of his dogs 'they had apparently only an imperfect consciousness, or inability to form correct notions, of the condition of the limb' (*op. cit.* p. 60). The term muscular sense as ordinarily understood, and as employed by these authors, is applied to the assemblage of centripetal impressions generated by the act of muscular contraction in the muscles themselves, as well as in the skin, fasciæ, ligaments, and joints. By the complex impressions so conditioned we judge of the fact and extent of muscular movement, either when we make the movements actively, or when our limbs are moved passively. The motor centres are, according to Hitzig and Nothnagel, the centres of this so-called sense. The destruction of the motor centres abolishes the perception of those impressions which accompany and guide muscular action, and hence the wavering and uncertain character of the movements actually effected. Even in dogs, however, as has been already indicated, the resemblance to ataxy is only a superficial one.

A more careful examination shows that those movements are least affected in which ataxy, when it exists, is most pronounced, viz. the movements of locomotion and similar co-ordinated acts; while those are most affected, or permanently rendered impossible, in which we recognise independence and true volition. Whatever may be said as to the condition in dogs, however, it is most certain that the term ataxy is not applicable to the effects of destruction of the motor zone in monkeys or in man. It is not in these a case of uncertainty or irregularity of movement, but an absolute paralysis and entire withdrawal of the part from the control of the will.

It is also certain—and a subject of daily clinical demonstration—that in paralysis from cortical disease the patient though unable to move his arm voluntarily is perfectly aware of every movement passively communicated to it, and can state with exactitude whether his arm is flexed or extended, whether his

[1] *Untersuchungen, supra cit.* [2] Virchow's *Archiv*, Bd. lvii. 1873.

fist is closed or open, and whether his finger is being flexed or extended gently or with force. His muscular sense, as well as every other form of common sensibility, is absolutely unimpaired. That he cannot move his arm does not arise from an imperfect or absent consciousness of his limb, but from destruction of an essential portion of his motor apparatus.

We have further already seen that the total abolition of the so-called muscular sense does not paralyse the power of effecting movements nor render them ataxic (p. 144). Even though the impressions ordinarily generated by muscular contraction are not perceived, yet the person can walk, or move his limbs, with perfect freedom under the guiding sense of vision. Even with the eyes shut the patient can intend his movements with correctness, but he may think that he has performed the intended movement though the limb has been held firmly or checked midway. There is no necessary connection between the power of directing movements and the muscular sense, as has been erroneously assumed by Brown-Séquard and others. Loss of the muscular sense never occurs without general anæsthesia of the limb. No one has ever furnished the slightest evidence of impairment or loss of the muscular sense apart from profound impairment or total abolition of the common sensibility of the limb. The statements to the contrary, sometimes met with, rest only on the foundation of a demonstrably false hypothesis as to the nature of the ataxy which it is invoked to explain.

As there is no evidence of impairment of the common sensibility of the limbs from destruction of the cortical motor zone, but conclusive evidence to the contrary, so are the views of Hitzig and Nothnagel respecting the abolition of the muscular sense equally without foundation. The existence of the so-called muscular sense does not confer mobility on the limb, for it exists in the limb paralysed as to motion either by spinal or cerebral lesion; nor does the absence of the muscular sense paralyse the limb as to motion or render its movements ataxic.

§ 17. Bastian [1] assumes that into the composition of the so-called muscular sense in addition to the cutaneous impres-

[1] *The Brain as an Organ of Mind*, 1880, p. 543.

sions, and those arising in the deep textures of the limbs during the act of muscular contraction, there enter also a 'set of "unfelt" impressions, which guide the motor activity of the brain by automatically bringing it into relation with the different degrees of contraction of all muscles that may be in a state of action' To these unfelt impressions he would give the name *kinæsthesis*, and he is of opinion that the so-called motor centres are in reality sensory, or the seat of this kinæsthesis, or sense of movement. The stimulation of these kinæsthetic centres acts in a manner reflexly by exciting the activity of the corpora striata or true motor centres.

In reference to this hypothesis I would remark that it is undoubtedly true that the due co-ordination of movements is largely conditioned by afferent impressions of an unconscious character, and that a disorganisation of the paths of these centripetal impressions is the main cause of ataxy. But inasmuch as perfect co-ordination is possible in the entire absence of the cerebral hemispheres, we have no reason for supposing that the cerebral centres are at all concerned in the mechanism of co-ordination. How unfelt impressions can enter into the composition of that which is so essentially a psychical act of discrimination is not very intelligible, nor how 'unfelt' impressions can be 'ideally' revived, or aid in the formation of a conception of the movement. Why the loss of the sense of movement, which in point of time should come after the movement, should render all movement impossible, as happens when the motor centres are destroyed in monkeys and man, is also incomprehensible. It might explain ataxy, but not paralysis. The theory that the cortical centres act only through the corpora striata is founded on an old and erroneous anatomy of the brain; for it has been conclusively demonstrated that the pyramidal tracts proceeding from the cortical motor centres do not join the corpora striata, but pass directly through, without any interruption in their continuity, to the anterior horns of the spinal cord. As these tracts degenerate centrifugally on destruction of the cortical centres, in precisely the same way as motor nerves on destruction of the anterior cornua, we have as good reason for applying the term motor to the cortical as to the spinal centres.

§ 18. It is, however, maintained by Bain,[1] Wundt,[2] and others that, apart from the feeling of movement effected, conditioned by centripetal impressions of the kind described, we have a feeling of force exerted, conditioned by the energising of the motor centres themselves. Bain says, 'As the nerves supplied to muscles are principally motor nerves, by which muscular movements are stimulated from the brain and nerve centres, our safest assumption is that the sensibility accompanying muscular movement coincides with the *outgoing* stream of nervous energy, and does not, as in the case of pure sensation, result from an influence passing inwards, by ingoing or sensory nerves' (*op. cit.* p. 92).

There is supposed to intervene between the intended movement and the actual carrying it into effect a feeling or sense of the motor innervation requisite for the desired end, which sense of innervation is supposed to be given in the energising of the motor centres themselves.

This hypothesis would make us conscious of the molecular processes of our brains. If true, we might have been able to evolve from our consciousness a knowledge of the motor centres which have only recently been discovered after much experimental and clinical research. Neither on subjective[3] nor ob-

[1] *The Senses and the Intellect*, 1864.

[2] *Physiologische Psychologie*, 1874.

[3] No one has put this more clearly than Professor W. James ('The Feeling of Effort,' *Anniversary Memoirs of the Boston Society of Natural History*, Boston, 1880), and his remarks are worthy of quotation *in extenso*. 'Now what can be gained by the interposition of this second relay of feeling between the idea and the movement? Nothing on the score of economy of nerve tracts; for it takes just as many of them to associate a million ideas with a million motor feelings, each specific, as to associate the same million ideas with a million insentient motor centres. And nothing on the score of precision; for the only conceivable way in which they might further precision would be by giving to a mind whose notion of the end was vague a sort of halting stage with sharper imagery on which to collect its wits before uttering its *fiat*. But not only are the conscious discriminations between "ends" much sharper than anyone pretends the shades of difference between feelings of innervation to be, but even were this not the case, it is impossible to see how a mind with its end vaguely conceived could tell out of a lot of *Innervationsgefühle*, were they never so sharply differentiated, which one fitted that end exactly, and which did not. A sharply conceived end will, on the other hand, directly awaken a distinct movement as easily as it will awaken a distinct feeling of innervation. If feelings can go astray through vagueness, surely the

jective analysis of cerebral processes does it seem necessary to superadd a sense of innervation to that which is contained in the idea of the movement; and it is certain that the motor centres have no concern in the process, for the idea of the movement may be most perfect when the motor centres are entirely destroyed. A dog with its motor centres destroyed has a clear idea of the movement required when asked to give a paw, and exhibits its grief at being unable to do so in an unmistakable manner; and the patient suffering from cortical motor lesion, after making futile attempts to carry out his ideally realised movement, not uncommonly bursts into tears at his failure.

There is no defect in the ideation, but only in the realisation of the movement.

§ 19. In favour of the existence of a consciousness of effort, apart from afferent impressions conditioned by muscular contraction, various considerations have been offered, some of which are of little weight. Of this kind are the experiments of W. Arnold [1] on the roots of the spinal nerves.

Arnold cut the posterior roots of the nerves of the frog's

fewer steps of feeling there are interposed, the more securely we shall act. We ought, then, on *a priori* ground alone to regard the *Innervationsgefühl* as a pure encumbrance.

'Let us turn now to *a posteriori* evidence. It is a notorious fact, recognised by all writers on voluntary motion, that the will seems concerned only with results, and not with the muscular details by which they are executed. But when we say "results" what is it exactly that we mean? We mean, of course, the movements objectively considered, and revealing themselves (as either accomplished or in process of being accomplished) to our sensible perceptions. Our idea, notion, thought, of a movement, what we *mean* whenever we speak of the movement, is this sensible perception which we get of it when it is taking place or has completely occurred. What, then, is this sensible perception? What does it introspectively seem to be?

'I unhesitatingly answer: an aggregate of *afferent* feelings, coming primarily from the contraction of the muscles, the stretching of tendons, ligaments, and skin, and the rubbing and pressing of joints; and secondarily, from the eye, the ear, the skin, nose, or palate, any or all of which may be indirectly affected by the movement as it takes place in another part of the body. The only idea of a movement which we *can* possess is composed of images of these its afferent effects. By these differences alone are movements mentally distinguished from each other, and these differences are sufficient for all the discriminations we can possibly need to make when we intend one movement rather than another' (p. 6).

[1] *Die Verrichtungen der Wurzeln der Rückenmarksnerven*, Heidelberg, 1844.

leg, and observed that when the animal was made to jump it used the leg operated on with apparently as much precision and energy as the sound one. From this the conclusion is drawn that the animal must still have retained the consciousness of muscular effort, otherwise it could not have used the limb in the manner described. We know, however, that the precision of the movements of locomotion in a frog is just as great when the cerebral hemispheres are entirely removed, and that bilateral reflex action of the limbs is easily produced in this animal by unilateral cutaneous stimulation. Psychical discrimination—a function which belongs to the hemispheres—forms no essential factor in the co-ordination of the frog's movements of locomotion. Arnold's experiment is nothing more than a very ordinary instance of bilaterally co-ordinated reflex action, and may be demonstrated in a frog deprived of its cerebral hemispheres, and therefore of all truly psychical faculties. To argue from the responsive or reflex actions of the frog to the conditions of psychical discrimination in man is not, I think, likely to lead to trustworthy conclusions. Certain facts observed in cases of hemiplegia in man, alluded to in the following quotation from Wundt,[1] are more to the point :—

'Whether the sensations accompanying the contraction of the muscles arise in the nerve fibres that transmit the motor impulse from the brain to the muscles, or whether special sensory fibres exist in the muscles, cannot be decisively settled. [See, however, p. 63.] Certain facts, however, make the first assumption more probable. If special nerve fibres existed they must be connected with special central cells, and thus in all probability the central organs for the apprehension of these sensations would be different from those which send out the motor impulse ; there would be two independent nerve systems—the one centripetal, the other centrifugal. But in the one, the medium of the sensation, nothing else could be regarded as the stimulus than the changes taking place in the muscle, the contraction, or perhaps the electrical process in nerve and muscle, accompanying the contraction. Now this process is known to keep equal pace with the energy of the

[1] *Menschen- und Thier-Seele*, Bd. i. p. 222.

muscular contraction, and we must expect that the muscular sensation would constantly increase and decrease with the amount of internal or external work done by the muscle. But this is not the case, for the strength of the sensation is dependent only on the strength of the motive impulse, passing outwards from the centre, which acts on the innervation of the motor nerves.'

Wundt then quotes instances of muscular paresis, or partial paralysis, where the patients are capable of feeling that they are putting forth great muscular effort, though the limb is hardly moved. This is a fact also commonly to be observed among hemiplegics, who express themselves conscious of putting forth great energy when told to move the paralysed limbs, though the limbs remain absolutely motionless.

A still more striking case of sense of effort, apparently conditioned by the outgoing current, is seen in cases of paralysis or paresis of the external rectus muscle of the eyeball. When, *e.g.*, the right external rectus is paralysed, the patient is unable to rotate the affected eye outwards. Yet, though the act of will has produced absolutely no movement of the eyeball outwards, the patient feels that he has given the proper innervation to the eyeball, and believes that the object flies to the right. When the external rectus is merely in a state of paresis or enfeeblement, and not completely paralysed, the same volitional stimulus which would move the eyeball to the extreme outer angle is able to effect only a very slight rotation outwards—say 20°. Yet though the eyeball has moved only 20° the patient believes that he has moved his eye to the extreme right. Inasmuch as the afferent impressions conditioned by a rotation of 20° must be the same in the paretic eye as in a sound one it is argued that the feeling of innervation must be a purely efferent one, varying with the degree of the motive impulse.

A little further inquiry, however, into the conditions coincident with the feeling of effort, exemplified in the above instances, speedily disposes of these plausible arguments. It is necessary that all movements whatever should be eliminated before we can admit that the sense of effort is conditioned by

the central motive impulse. For in the fact of associated muscular action, and the concomitant centripetal impressions, even though not expressly willed, the conditions of the consciousness of effort exist, without our being obliged to regard it as dependent on central innervation or outgoing currents. Now though the hemiplegic patient cannot move his paralysed limb, and is nevertheless conscious of putting forth great effort, he will be found to be making powerful muscular exertion of some kind. Very often he will be seen to be making with his sound limb the movement which he is desirous to effect with his paralysed limb. Observers of the phenomena associated with the paralysed or paretic external rectus have, as W. James [1] has shown, failed to note what is taking place in the associate internal rectus of the sound eye. The conjugate movements of the eyeballs—the external rectus of the one eye and the internal rectus of the other—are innervated from a common centre, and we are unable to discriminate between the sensations arising from each individually. Now when the patient is unable to move the affected eye outwards at all, or only partially, he is making strong convergent movement of his sound eye, and he estimates the direction of the object precisely in accordance with the degree of contraction of the internal rectus of this eye. The sense of innervation is clearly dependent on the strain on the internal rectus of the sound eye, and not on the central motive impulse. Even when the associated movements are not so obvious as in the cases above alluded to, it is not difficult to discover the basis of the sense of effort in the centripetal impressions generated by some form of active muscular exertion.

If the reader will extend his right arm and hold his forefinger in the position required for pulling the trigger of a pistol, he may, without actually moving his finger, but by simply making believe, experience a consciousness of energy put forth. Here, then, is a clear case of consciousness of energy without actual contraction of the muscles either of the one hand or the other, and without any perceptible bodily strain. If the reader will again perform the experiment, and pay careful attention to the condition of his respiration, he

[1] *Op. cit.*

will observe that his consciousness of effort coincides with a fixation of the muscles of his chest, and that, in proportion to the amount of energy he feels he is putting forth, he is keeping his glottis closed and actively contracting his respiratory muscles. Let him place his finger as before, and *continue breathing* all the time, and he will find that, however much he may direct his attention to his finger, he will experience not the slightest trace of consciousness of effort until he has actually moved the finger itself, and then it is referred locally to the muscles in action. It is only when this essential and ever-present respiratory factor is, as it has been, overlooked that the consciousness of effort can with any degree of plausibility be ascribed to the outgoing current. In the contraction of the respiratory muscles there are the necessary conditions of centripetal impressions, and these are capable of originating the general sense of effort. When these active efforts are withheld no consciousness of effort ever arises, except in so far as it is conditioned by the local contraction of the group of muscles towards which the attention is directed, or by other muscular contractions called unconsciously into play in the attempt.

I am unable to find a single case of consciousness of effort which is not explicable in one or other of the ways specified. In all instances the consciousness of effort is conditioned by the actual fact of muscular contraction. That it is dependent on centripetal impressions generated by the act of contraction I have already endeavoured to show. When the paths of the centripetal impressions, or the cerebral centres of the same, are destroyed there is no vestige of a muscular sense. That the central organs, for the apprehension of the impressions originating from muscular contraction, are different from those which send out the motor impulse has already been established. But when Wundt argues that this cannot be so, because then the sensation would always keep pace with the energy of muscular contraction, he overlooks the important factor of the fixation of the respiratory muscles, which is the basis of the general sense of effort in all its varying degrees. In the first instance, our consciousness of the extent and energy of our muscular contractions, and the faculty of

muscular discrimination, are derived from the centripetal impressions generated by the contraction itself. The association of the sensory impression with the corresponding movement, however, becomes by education so precise, and the nexus so firmly welded, that we can apparently by intuition estimate the exact degree and extent of movement necessary to accomplish any desired end.

§ 20. It is further possible, by reviving the sensory impression, to recall in idea the movement which coincided with it, even though the muscles themselves, to which the movement is referred, have been severed from the body. Many remarkable instances of this kind have been given by Weir-Mitchell.[1]

'If we faradise the track of the nerves in or above the stump, we may cause the lost fingers and thumb to seem to be flexed or extended, and, what is most remarkable, parts of which the man is conscious, but which he has not tried to stir for years, may thus be made to appear to move, to his utter amazement. In one case I thus acted on the nerves so as to cause a thumb, which for years was constantly and violently bent in on the palm, to straighten out completely. On breaking the circuit, without warning, the patient exclaimed that his thumb was cutting the palm again, and the same result was obtained by shifting the conductors, so as to put the nerves out of the circuit. In a case of amputation of the shoulder-joint, in which all consciousness of the limb had long since vanished, I suddenly faradised the brachial plexus, when the patient said at once, "My hand is there again; it is bent all up, and hurts me." These impressions are correctly referred by the patient, so that the faradisation of the musculo-spiral or the ulnar gives sensation of movement in the related parts. It is, of course, impossible that the motor nerves stimulated should convey any impression centrally; and we must conclude that irritation of sensory trunks may occasion impressions of muscular action in the sensorium' (*op. cit.* p. 359).

The excitation of the sensory nerves calls up, as Weir-Mitchell correctly indicates, the correlated movement, i.e. the

[1] *Injuries of Nerves*, 1872.

movement which in the actuality of past experience had coincided with the sensation now revived by the faradic stimulus. This of itself argues powerfully in favour of the centripetal origin of the impressions constituting the muscular sense. According to the law of contiguity, 'actions, sensations, and states of feeling, occurring together or in close succession, tend to grow together, or cohere, in such a way that when any one of them is afterwards presented to the mind the others are apt to be brought up in idea.' The ideal associated movement is thus made to arise in consciousness, when the corresponding sensation is artificially re-excited. But the register of sensory impressions is anatomically distinct from that of movements, and the two cohere together only by constant functional association.

Inasmuch as the idea of a movement is only an idea of the sensory impressions, visual, tactile, and others, which coincide with the particular movement, it seems quite possible that persons who have had a limb amputated may be able to picture a movement of the limb, just as a blind man may recall a scene when he can no longer see. That this in reality occurs is likewise shown by Weir-Mitchell. 'Persons who have had an arm amputated are frequently able to will a movement of the hand, and apparently to execute it to a greater or less extent. A small number have entire and painless freedom of motion as regards all parts of the hand. "My hand is now open, or it is shut," they say. "I touch the thumb with the little finger," "The hand is now in the writing position," &c. Between these cases and such as are conscious of an immobile member every grade of difference as to motion is to be found, with equally wide varieties in the associated pain, which perhaps is most acute in such as will with vigour a motion that they seem to fail in executing' (p. 357). In some of these cases the muscles which move the hand remain, and, therefore, are excluded from consideration in the present relation. 'In others, as in shoulder-joint cases, or amputations through the humerus, the muscles which act on the hand are absent altogether; yet in these there is fully as clear and definite a consciousness of the movements of the fingers, and of their change of positions, as in the former cases.'

These facts are supposed by Weir-Mitchell, and also by Hughlings-Jackson,[1] to favour the views of Bain and Wundt as to the dependence of the sense of innervation on the outgoing current. They however, in my opinion, only indicate a vivid realisation of sensory impressions associated with a particular movement, and have nothing to do with the motor centres or outgoing currents. A patient suddenly paralysed by embolic softening of his motor centres not unfrequently only discovers his paralysis by being unable to carry out the movement which he has willed, and of which he has formed a distinct conception. The act of volition does not imply movement, or the ability to carry it out, nor does the conception of the movement depend on the integrity of the motor centres. Volition is effected when the idea of the movement, formed in the sensory centres, is permitted to operate, even though the active manifestation is rendered impossible by destruction of the motor apparatus necessary for its accomplishment. There is no more reason why we should not be able to revive in idea past movements through the associated sensations, when the limb by which the experience was gained is amputated, than recall visual impressions after extirpation of the eyeballs. But, as we cannot any longer see when the eyes are destroyed, so we can no longer exercise muscular discrimination, or gain musculo-sensory experience, when the limbs are amputated. We retain what we have already acquired, but make no further advance. But, whether we make the movements in reality or revive them in idea, the consciousness of the extent and energy of the movements is, in my opinion, in all cases dependent on ingoing or centripetal impressions. In the case of actual movements the impressions arise directly in the periphery; in the case of ideal movements the sensory impressions arise by excitation of the centres which form the organic register of impressions primarily originating in the periphery.

The centres of centrifugal, or motor, impulses are anatomically distinct from those of centripetal, or sensory, impressions. The one may be destroyed, while the other remains intact.

[1] *Med. Journal*, leading article, Oct. 9, 1875.

The cortical centres, for the movements of the limbs, are concerned purely with centrifugal impulses, and are clearly differentiated from the paths and terminal centres of the centripetal impressions on which muscular discrimination is based.

The destruction of the centripetal centres abolishes muscular sense, or muscle consciousness, though the power of movement remains. The destruction of the centrifugal centres abolishes the power of voluntary motion, and therefore prevents the exercise of muscular discrimination, but the transmission and perception of centripetal impressions continue unimpaired.

§ 21. It would be a crucial test of the dependence of the muscular sense on centripetal impressions if it could be shown without fallacy that muscular discrimination can still be exercised when the muscles are made to contract artificially by means of the electric stimulus. Experiments on this point have been made by Bernhardt[1] but, owing to the difficulty of excluding the sense of cutaneous pressure, he came to no positive conclusions. Though Bernhardt himself is inclined to regard the muscular sense as a 'Function der Seele,' only aided by centripetal impressions, his experiments show that differentiation of weights can be made when the muscles are excited to contraction by the electric current alone. 'Normal individuals, however,' says he, 'discriminate equally well when the flexion of the finger, and thereby the raising of the weight, was caused by the electric current.'

According to the law of perception of weight by the sense of cutaneous pressure alone, it requires the addition of one-third of the original weight, whatever it may be, to produce a distinctly perceptible difference; but in Bernhardt's experiments on the foot it was found that the addition of from 3 to 5 Loth ($1\frac{1}{2}$ to $2\frac{1}{2}$ oz.) to an original weight of from a pound to a pound and a half could be distinctly perceived, which is less than one-half the increment perceptible by cutaneous pressure alone.

In regard to the discrimination of weight by the finger the sensibility was found to be much finer. Three drachms could

[1] *Archiv f. Psychiatrie*, Bd. iii. 1872.

be distinctly differentiated from nothing, and to heavy weights (say 1 lb.) the addition of five drachms was distinctly perceived, i.e. a difference of about $\frac{1}{16}$, a power of discrimination which corresponds pretty nearly with that of the muscular sense, which is capable of detecting an addition of $\frac{1}{17}$th of the original weight. These results, therefore, indicate that the discrimination was much finer than could be effected by the sense of pressure alone, and that, therefore, it depended on muscular discrimination.

Experiments made in reference to this point by myself, with the assistance of Dr. Lauder-Brunton, gave such results as clearly to indicate the retention of muscular discrimination when the muscles were excited to contract by the galvanic current. The method I adopted was to determine, blindfolded, in the first instance, the differences in weight which could be discriminated by my hand held flat on a cushion, and then to test the muscular discrimination of the same weight when the wrist was flexed so as to raise the weight with the fingers. By repeated experiments with weights varying from one to six ounces the average discrimination by the sense of cutaneous pressure was found to be about one-third, while the muscular discrimination accorded pretty nearly with the 1-17th, as usually found to be the rule.

The same experiments were then made with the same hand as regards cutaneous pressure, and by galvanic excitation of the flexor muscles of the hand, so applied as to cause repeated raising of the weight by the fingers. Again the sense of pressure averaged the normal, and again muscular discrimination was found to be almost as accurate as in the former experiments, when the raising of the fingers depended on voluntary effort.

Cutaneous pressure being thus allowed for in both cases, the muscular discrimination by means of the centripetal impressions generated by muscular contraction alone, not depending on voluntary motor impulse, is clearly established.

It is also a very important fact, noted by Leyden (Virchow's 'Archiv,' xlvii.) that ataxic patients, who are said to retain muscular discrimination notwithstanding the abolition of cutaneous sensibility, are not able to discriminate weights

until they reach a considerable amount. It is supposed that this is due only to a diminution, owing to the absence of the usually associated sensations of pressure. But I am of opinion that the discrimination of heavy weights calls into play the general sense of effort which, as we have seen, is to be more properly ascribed to the region of the respiratory muscles; and that the discrimination in this case is effected by the amount of bodily strain and fixation of the muscles of the chest necessary to support a heavy weight; and that it is not a question of the muscular sense of the limb at all, unless general strain is absolutely eliminated by continuous and easy respiration during the trial. When this is eliminated it will be found that the sense of local resistance is the only element in the discrimination of weight.

The various considerations above advanced seem to me to prove beyond all doubt that the motor centres are not the centres of the so-called muscular sense, whether we understand this as a sense composed of a complex assemblage of centripetal impressions, or as a sense of innervation according to the views of Bain and Wundt. The cortical centres are motor in precisely the same sense as other motor centres, and are differentiated anatomically from the centres of sensation, general as well as special.

The Frontal Motor Centres.

§ 22. Electrical stimulation of the frontal lobes varies according to the position of the electrodes. Irritation of area (12) comprising the base of the superior and middle frontal convolutions in monkeys, and the corresponding region in other animals, gives rise to lateral movement of the head and eyes to the opposite side, with dilatation of the pupils. The expression assumed by the animal is that of attention or surprise. The same movement occurs, along with other special reactions, also on stimulation of the angular gyrus, and of the superior temporo-sphenoidal convolution more especially. With the latter is associated pricking of the ear, the special sign of stimulation of the auditory centre. The reactions were found to be essentially the same in all the

animals experimented on, varying, however, in degree. If we assume, as will be proved subsequently, that the frontal centre—(12)—is the true motor centre for the lateral movement of the head and eyes, and as such the centre for movements expressive of attention, it would be natural to expect that the arousal of subjective sensations by stimulation of the visual and auditory centres would excite attention, and induce the same movements of the head and eyes as would result from direct stimulation of the motor centre. In the one case the reaction is the result of stimulation of the motor centre directly, in the other only indirectly or reflexly by stimulation of a sensory centre proper.

As a rule, I have found stimulation of the prefrontal regions and other portions of the frontal lobes to be entirely negative, or so irregular as to render the results very doubtful. In particular the approximation of the electrodes to the anterior extremity of the hemisphere is apt to cause irritation of the olfactory bulbs, and thus give rise to active reflex reactions which may be erroneously ascribed to the frontal lobes themselves.

Yet in two instances I have noted movements of the eyeballs on irritation of the prefrontal regions under circumstances entirely precluding diffuse irritation of neighbouring parts. The eyeballs were seen during irritation to move sometimes laterally to the opposite side and sometimes upwards. Whether the movements of the eyes in these two cases were only coincidences, or causally related to the irritation of the frontal lobes, is not quite certain, but I am inclined to regard them as of the latter character.

§ 23. The effects of destructive lesions are not yet sufficiently definite to enable us to speak with certainty regarding the functions of the frontal lobes in all their parts. But there is sufficient evidence to show that the postfrontal regions—area (12)—are the motor centres of the lateral movements of the head and eyes. It has frequently been observed in man that, for a short period after the onset of sudden hemiplegia, the head and eyes are turned away from the paralysed side, looking, therefore, towards the side of lesion. The same thing occurs in the monkey. At the moment of destruction of area (12) in

the one hemisphere [1] there occurs a conjugate deviation of the eyes towards the side of lesion. If the transitory duration of this deviation were due only to the compensatory action of the sound hemisphere it would follow that destruction also of this centre should cause permanent inability to turn the head or eyes in either direction. But this is not the case even when the destruction of area (12) in both hemispheres is very extensive, if not absolutely complete.

In two monkeys [2] after extensive bilateral destruction of the base of the superior and middle frontal convolutions, though for the first day after the operation there was evident inability to turn the head or eyes in either direction, as well as some oscillation of the head (in the one in which the lesion was the more extensive), yet within a few days at most the power of turning the head and eyes in either direction, without any appearance of unsteadiness or stiffness, was seen to have been regained. At first the animals did not look round to sounds in proximity to the ear, as usual, or if they did they moved the trunk and head *en masse*. The complete recovery cannot be accounted for altogether by incomplete destruction of the postfrontal centres, for the lesions were sufficient to have left very visible permanent results if these were the whole of the centres of the movements in question.

I had already in my former experiments noted the extraordinary absence of any discoverable physiological defect after entire removal of the prefontal lobes or anterior half of the frontal lobes.[3] And in one case [4] also, in which the occipital lobes had been removed some time previously, the removal of both prefrontal lobes was likewise unattended by any evident sensory or motor impairment (see fig. 88).

I have again confirmed these observations. In a monkey [5] I destroyed with the galvanic cautery the whole of the prefrontal region on both sides in advance of area (12), so that, except a minute portion of each frontal lobe overlying the

[1] *Phil. Trans.* Part II. 1884, p. 530.
[2] Experiments 19 and 20, *Phil. Trans.* Part II. 1884, p. 521 *et seq.*
[3] Experiments I., II., III., *Phil. Trans.* Part II. 1875.
[4] Experiment XXV., *ibid.*
[5] Experiment 22, *Phil. Trans.* 1884, p. 525.

olfactory bulbs, all the intervening portion of the superior, middle, and inferior frontal convolutions was obliterated (fig. 121). Notwithstanding this extensive bilateral lesion there was a total absence of symptoms either in the domain of motion or sensation. The animal perceived a touch anywhere on the body, the special senses were intact, and the movements of the head and eyes were in all respects unimpaired.

A similar total absence of discernible symptoms has been observed also by Horsley and Schäfer [1] on destruction of the prefrontal regions in two monkeys which survived the operation for many months. There was certainly no affection of the movements of the trunk.

§ 24. In one case,[2] however, in which the paralysis of the

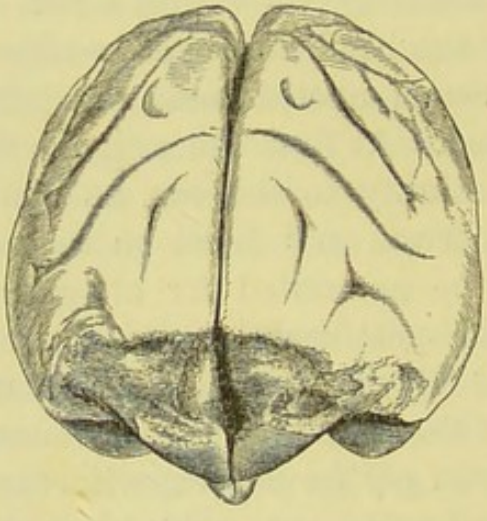


FIG. 121.—Lesion of the Prefrontal Region.

lateral movements of the eyes, following lesion of the post-frontal centres, had completely disappeared, the destruction also of the prefrontal regions caused symptoms which, though transient, were of great significance. These were rapid oscillations of the head, apparent inability to turn the head, except *en masse* with the trunk, and drooping of the right eyelid. By the third day, however, all these symptoms had disappeared, and from this time onwards the animal exhibited no defect either as regards its powers of motion or sensation. The lesions in this case were extensive erosion of the cortex at the posterior third of the three frontal convolutions, with complete

[1] Private communication.

[2] Experiment 23, *Phil. Trans.* 1884, p. 530, figs. 74-86.

removal of the anterior two-thirds of the inferior and middle, and portion of the superior frontal convolution, on the left side; and complete removal of the middle frontal and anterior two-thirds of the inferior frontal convolution on the right side.

These facts indicate that the prefrontal regions belong to the same centres as the postfrontal, just as the occipital lobes belong to the visual centres; for though the occipital lobes do not react to electrical stimulation, and may be removed without any appreciable disturbance of vision, provided the angular gyri remain intact, yet it has been seen that they form an integral portion of the visual centres. So, though the prefrontal regions do not react, or doubtfully, to electrical stimulation, and their removal causes no discoverable symptoms, provided the postfrontal regions are intact, yet as their removal induced effects similar to those resulting from the previous lesion of the postfrontal regions, it may be argued reasonably that they form part of the same centre. The transitory duration of the symptoms, even when the whole frontal region was more or less considerably injured, would be explained by the fact that the postfrontal centres were not entirely destroyed on either side, and less completely on the right than on the left. On the side opposite the more extensive lesion there was a tendency to ptosis of the eyelid as well as inability to turn the eyes laterally.

To determine whether the complete removal of the frontal regions—postfrontal as well as prefrontal—induces permanent paralysis of the lateral movements of the head and eyes is not an easy matter. A frontal incision through the base of the frontal convolutions, and complete scooping out of the frontal lobes, involves injury to the head of the corpus striatum on each side. The operation is also a serious one. In the only case[1] in which I performed this experiment the animal died suddenly twenty-four hours after the operation. But the facts are worthy of consideration. Both frontal lobes were severed by a frontal incision immediately anterior to the præcentral sulcus. The portions removed included the anterior extremity of the nucleus caudatus, somewhat more on the left side than the right.

[1] Experiment 21, *Phil. Trans.* 1884, p. 524, figs. 58, 59.

Notwithstanding the formidable character of the operation, the animal speedily regained consciousness, and was able to move its facial muscles and the limbs, though the right limbs were used with somewhat less energy than the left. Though it could in some degree extend its head and trunk, it was utterly unable to maintain the upright position or move its head and eyes laterally. The eyes were kept shut except on cutaneous or other sensory stimulation. Sight, hearing, and tactile sensibility were unimpaired. Except the inability to move the head and eyes there was no other defect observable, sensory or motor. Though, as remarked, the injury to the corpora striata somewhat complicated the lesion, and the duration

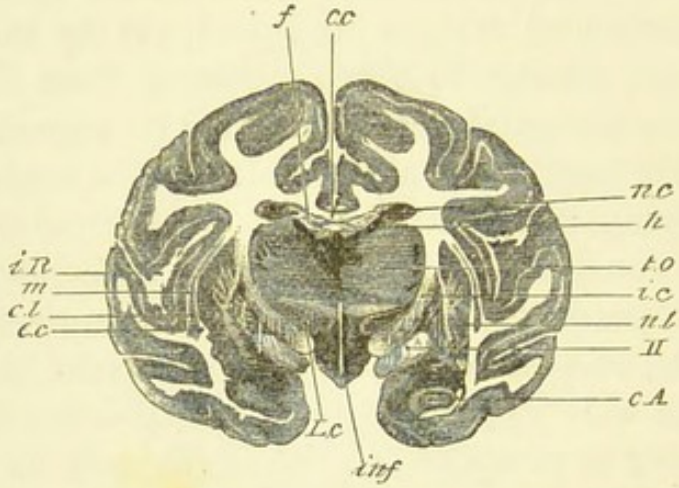


FIG. 122.—Frontal Section of the Brain (fig. 121), showing degeneration of the mesial fibres of the internal capsule on both sides, consecutive to lesion of the prefrontal regions. The degenerated fibres are indicated by white patches on each side of the infundibulum and third ventricle.

of the period of observation was but short, yet the hypothesis that this portion of the brain is specially concerned in the movements of the head and eyes, indicated in the other experiments, is confirmed. For no other movements were paralysed, and there was no affection of vision, hearing, or common sensibility in any part of the body.

§ 25. In two of the experiments facts were demonstrated of great importance in reference to the anatomical connections of the frontal lobes. In the one of these,[1] in which the prefrontal regions had been almost completely extirpated (fig. 121), and which survived in perfect health for nearly three months

[1] Experiment 22, *Phil. Trans.*, Part II., 1884, p. 525, figs. 60–73.

after the operation, microscopical examination revealed the existence of descending sclerosis in the innermost or mesial bundles of the internal capsule and foot of the crus cerebri on either side (fig. 122). These degenerated tracts could not be traced beyond the upper part of the pons, and therefore their exact destination could not be determined, but they were not traceable in the anterior pyramids of the medulla oblongata.

In the other [1] the postfrontal centres had first been extensively destroyed, and seven weeks afterwards the prefrontal regions were more or less completely removed. At the end of two months and a half after the first operation degeneration had also occurred in the same mesial bundles of the internal capsule and foot of the crus. The degenerated bundles were from their appearance of different dates. Those situated somewhat external to the most mesially placed bundles were deeply sclerosed, corresponding to the older of the two lesions, viz. of the postfrontal lobes. The most internal bundles, corresponding exactly in position to those of the previous experiment, were of more recent date, and less densely sclerosed, in relation with the later lesions of the prefrontal centres.

We have in these facts a proof of the anatomical relation of the frontal lobes to the motor tracts of the crus cerebri, and inasmuch as no degeneration existed in the anterior pyramids it is clear that the tracts with which they are in connection do not extend below the medulla oblongata. Confirmation is thus given to the conclusion, founded on the symptomatology, that the frontal centres are concerned with the movements of the head and eyes, the nuclei and motor nerves of which do not extend below the medulla oblongata.

Even though in the first experiment the destruction of the prefrontal regions caused no discoverable physiological defect, yet secondary degeneration occurred in the internal capsule. That the functions subserved by these centres and tracts were practically unimpaired would show that the centres for these movements were not entirely destroyed; and that the prefrontal and postfrontal regions form parts of the same centre, is supported by the facts of degeneration as observed

[1] Experiment 23, *op. cit.* p. 528, figs. 74-86.

in the second experiment, as well as by the circumstance that injury to the prefrontal regions reinduced for a time the disturbances which had temporarily manifested themselves after lesion of the postfrontal centres.

We have thus good reasons for regarding the frontal lobes as in anatomical relation with motor tracts which do not pass into the spinal cord, but end in the centres of the mesencephale or bulb.

§ 26. Munk[1] professes to have found that, after destruction of the prefrontal region in dogs and monkeys, paralysis occurs in the muscles of the trunk on the opposite side, so that the animal is unable to turn to this side; and that bilateral destruction causes paralysis of the trunk muscles on both sides, so that the animal can turn neither to the right nor to the left.

Though he furnishes no evidence of impaired sensibility in the trunk or elsewhere, he nevertheless calls the prefrontal region the sensory sphere (*Fühlsphäre*) of the trunk. Munk's assertions as to the effects of lesion of the prefrontal region have as little foundation as many other of his utterances on cerebral physiology. My own experiments, as well as those of Horsley and Schäfer, disprove Munk's assertions in the case of monkeys, and clinical observations[2] show that in respect to man they are equally untrue.

In regard to dogs Munk is flatly contradicted by Hitzig,[3] Kriworotow,[4] and Goltz.[5] Not one of these physiologists has observed any of the motor disturbances described by Munk, after entire removal of the prefrontal regions. Kriworotow says that in all his dogs the mobility of the trunk, trunk muscles, and lumbar vertebræ was absolutely unimpaired, whether one or both prefrontal regions were destroyed.

Goltz relates that in one dog he removed the whole of the region lying in front of the crucial sulcus on both sides. Yet

[1] *Die Functionen der Grosshirnrinde*, 1881, 4te Mittheilung, und *Die Stirnlappen des Grosshirns*, 1883.

[2] See *Localisation of Cerebral Disease*, 1878.

[3] *Neurologisches Centralblatt*, July 1883; *Archiv f. Psychiatrie*, Bd. xv. p. 270.

[4] *Die Functionen des Stirnlappens des Grosshirns*, Thèse, 1883.

[5] 'Die Verrichtungen des Grosshirns,' Pflüger's *Archiv*, Bd. xxxiv. 1884.

this animal was able to turn its trunk so well as to be able to seize a piece of meat attached to the root of its tail. In numerous other cases in which the prefrontal regions were removed, in addition to extensive lesion of the motor zone proper, there *never* occurred such affection of the trunk muscles as Munk describes.[1] It is unnecessary to adduce further evidence of Munk's untrustworthiness. If the description he gives of his experimental results is correct, they can only be attributed to crude methods and widespread secondary disturbances. Horsley and Schäfer have shown that the centres for the trunk muscles are in the marginal convolutions. It is only to primary or secondary implication of these marginal centres, and not to lesions strictly limited to the prefrontal regions, that we can ascribe such results as Munk claims to have observed.

§ 27. Besides the physiological symptoms, such as occur, and the descending degenerations of the motor tracts associated with lesions of the frontal lobes, I observed and recorded[2] certain symptoms indicative of mental deterioration which have since been confirmed by other physiologists.

In my first series of experiments (carried out without antiseptics) I noted after removal of the prefrontal regions a decided alteration in the animals' character and behaviour, but difficult to describe precisely. After the operation, though they might seem to one who had not compared their present with their past fairly up to the average of monkey intelligence, they had changed considerably. Instead of, as before, being actively interested in their surroundings, and curiously prying into all that came within the field of their observation, they remained apathetic or dull, or dozed off to sleep, responding only to the sensations or impressions of the moment, or varying their listlessness with restless and purposeless wanderings to and fro. While not absolutely demented, they had lost, to all appearance, the faculty of attentive and intelligent observation.

In some of my later experiments,[3] in which the lesions were strictly limited (under antiseptic precautions) to the pre-

[1] *Op. cit.* p. 485. [2] *Phil. Trans.*, Part II. 1875.
[3] *Phil. Trans.*, Part II. 1884.

frontal regions I could not satisfy myself of the existence of any appreciable mental deterioration, but in others the same listlessness and purposeless unrest previously observed were apparent in greater or less degree. Probably the differences were dependent on the degree of implication of the frontal lobes as a whole. In the experiments under antiseptic precautions the area of secondary disturbance would naturally be much less extensive than in those in which no antiseptics were employed.

Horsley and Schäfer have also noted signs of stupidity in the monkeys in which they had removed the prefrontal regions —for a time at least after the operation.

Hitzig[1] observed decided mental deterioration in dogs after destruction of the prefrontal regions. Dogs which before the operation had been in the habit of finding their food on a table, seemed quite unable to do so after bilateral destruction of the prefrontal region. 'They exhibited such a marked weakness of memory (*Gedächtnissschwäche*) that they quite forgot the existence of the pieces of meat they had just seen. They, however, ate pieces of meat thrown before them, so long as they saw them; but they did not search for their food in the accustomed place like normal dogs. Besides these they exhibited other alterations in their behaviour which I will not enter on more fully at present' (p. 271).

Goltz[2] observed that dogs after removal of the frontal regions exhibited, among other symptoms, great irritability and restlessness. They could see, hear, smell, and taste, but reacted in many respects differently from normal animals. All the animals so experimented on had 'a fixed and stupid expression of the eyes, and inability to fix the gaze.' 'They are,' says he, 'able to perceive and recognise persons and things at great distances. They understand also a threatening gesture with the hand or with a whip, inasmuch as they wince, but they show no inclination to run away, and make no sound indicative of fear. If the finger is thrust towards the eye they only shut the eyelids when the finger actually touches the eyelashes. Very remarkable is the following experiment

[1] *Archiv f. Psychiatrie*, Bd. xv. p. 271.

[2] Pflüger's *Archiv*, Bd. xxxiv. 1884.

which I have made on several dogs. If a bone is thrown down to the animal at some distance, it runs to it with great alacrity, but does not have the sense to stop at the right moment and sink its head, so that it runs beyond the mark. Instead, however, of turning round and looking for the bone in a methodical way, the animal appears to forget what it was after, and runs on regardlessly, until the bone is lifted and the animal's attention again attracted to it' (*op. cit.* p. 481).

The observations of Hitzig and Goltz appear to me to illustrate and confirm the occurrence of a mental deterioration from lesion of the prefrontal regions, which I have characterised as essentially a defect of the faculty of attention. What relation these symptoms have to the anatomical substrata of the frontal regions will be the subject of consideration in another chapter (Chapter XII., § 17).

CHAPTER XI.

FUNCTIONS OF THE BASAL GANGLIA.

§ 1. The position and relations of the basal ganglia—the corpora striata and thalami optici—have already been discussed (Chapter I. § 10), and we have seen that their relations have not yet been in all respects satisfactorily determined. With respect to the corpora striata the most recent investigations are opposed to the view propounded by Meynert that they are 'ganglia of interruption' intercalated in the projection system between the cortex and the periphery. We have seen that the pyramidal strands of the internal capsule pass directly from the cortical motor zone to the pyramids of the medulla oblongata without interruption in the grey matter of the corpora striata, either of the lenticular or caudate nuclei. It is doubtful whether any fibres of the corona radiata connect the cortex with the base of the lenticular or caudate nucleus. If so they are relatively much fewer than Meynert supposed. It is much more probable that the ganglia of the corpus striatum are in themselves terminal centres similar to those of the cortex itself. The tracts which proceed from the nucleus caudatus first cross those of the internal capsule and enter the two inner divisions of the lenticular nucleus, and emerge with those derived from the lenticular nucleus itself. These form two main divisions. The one division, the smaller, joins the internal capsule, and lies dorsally to the pyramidal tracts in the foot of the crus. The fibres appear to end in the region of the locus niger or to form connections with the centres of the pons. The other division constitutes a well-marked tract, visible on the internal margin of the crus cerebri in the anterior perforated space, and termed the

lenticular loop (*ansa lenticularis*). This, according to Flechsig, is connected on the one hand with the red nucleus (fig. 19, R N), and thus indirectly with the cerebellum through its superior peduncle; and on the other hand with the lemniscus derived from the interolivary layer, and thus indirectly with the olivary bodies, and perhaps also with the clavate and cuneate nuclei.

As the functions of the various tracts and centres with which the corpora striata appear to be related are not in themselves well known, little with respect to the functions of the corpora striata can be founded merely on their anatomical relations. But the fact that the greater portion of the lemniscus—that portion which is specially connected with the corpus striatum—degenerates in a centrifugal direction is an important indication of motor function.

§ 2. The connections of the optic thalami are more uncertain than those of the corpora striata. Connections have been traced through the corona radiata with various regions of the cortex, viz. the frontal, parietal, occipito-temporal, region of the insula, and with the hippocampal region by means of the pillars of the fornix, either directly, or indirectly through the corpora mammillaria. The longitudinal tracts of the tegmentum, which by some have been regarded as ending in the optic thalami, are traced by Flechsig past these ganglia into the posterior part of the internal capsule. On this point, however, and on many others, the views of different anatomists are so divergent that it would be unsafe to found any functional relationship on anatomical data. Besides the connections with the cortex and the tegmentum others have been traced between the optic thalami and the corpora striata.

Luys[1] describes the optic thalamus as consisting of an agglomeration of centres—an anterior, middle, median, and posterior—connected on the one hand with definite regions of the cortex, and with the olfactory, optic, general sensory, and auditory tracts respectively. The views of Luys have been regarded by most anatomists[2] as purely speculative and devoid of any foundation in demonstrated fact. But Gudden[3]

[1] 'The Brain and its Functions,' *Internat. Scient. Series*, vol. xxxvii. 1881.
[2] Schwalbe, *Neurologie*, p. 713. [3] *Archiv f. Psychiatrie*, Bd. xi.

has shown that after removal of the cortical centres in their entirety the corresponding optic thalamus entirely atrophies, while the corpus striatum remains intact. Ganser [1] also distinguishes four separate centres in the optic thalamus of the mole; and more recently Monakow [2] has differentiated several distinct centres in the optic thalamus of the rabbit, and contends that destruction of certain circumscribed cortical regions leads to atrophy of the correlated nuclei (see further § 9).

§ 3. The experimental investigation of the functions of the basal ganglia is also surrounded with special difficulties. Owing to their position they can only be reached by exposing the interior of the lateral ventricles, or by inflicting injury on some portion of the cortex and the tracts which surround them or pass through them. Hence the effects of experimental lesions of the basal ganglia are always more or less complicated by the injuries necessarily inflicted on other parts, in the attempts to reach them, some of which are incompatible with long survival.

We are largely dependent on the data of clinical medicine for what we know respecting the effects of lesions of the basal ganglia. Owing to the mode of their vascular supply by the lenticulo-striate and lenticulo-optic arteries they are a favourite and frequent seat of embolic softening; but the lesions so induced are rarely so precise in their limitation to the ganglia proper, apart from the merely transcurrent tracts of the internal capsule, as to afford altogether reliable data for determining their special functions.

For purposes of electrical stimulation it is not difficult to reach the surface of the basal ganglia by division of the corpus callosum and exposure of the interior of the lateral ventricle. But in doing so it is necessary to guard against the occurrence of hæmorrhage and shock, otherwise erroneous conclusions may be drawn respecting the excitability of these structures. Just as the excitability of the cortex is liable to be annihilated by profound narcosis, shock, and hæmorrhage, so the excitability of the basal ganglia is liable to be affected by similar circumstances. The most favourable conditions for

[1] *Das Gehirn des Maulwurfs*, 1880. See also fig. 35.

[2] *Archiv f. Psychiatrie*, Bd. xii. 1882.

the investigation of the electric excitability of the basal ganglia are furnished by those cases in which after successive exposure and electrical exploration of the different regions of the convexity the corpus callosum is divided, and the hemisphere easily everted, so as clearly to expose the interior of the lateral ventricle. Under such circumstances, I have, as before related, found that electrical irritation of the intraventricular nucleus of the corpus striatum causes tonic contraction of the whole of the muscles of the opposite side, resulting in a condition of pleurosthotonus, in which the position assumed is that of equilibrium between the flexors and extensors. In rabbits, however, the tonic spasm was not so rigidly maintained, and during the continuance of the stimulation the jaws were constantly ground together. Shifting of the electrodes on to the ventricular aspect of the optic thalamus at once caused cessation of the tonic spasm and an entire absence of all visible results. In only one rabbit was there any sign of irritation, consisting in general shuddering and restlessness, such as might be regarded as indications of general sensory excitation.

The experiments of Carville and Duret[1] are in entire harmony with mine. They observed general spasm of the muscles of the opposite side on irritation of the caudate nucleus and an entire absence of outward manifestation when the surface of the optic thalamus was similarly irritated by the faradic current. It has, however, been contended by some experimenters[2] that neither the corpora striata nor the optic thalami are themselves excitable, and that such movements as result from so-called irritation of the nucleus caudatus are in reality due to irritation of the fibres of the internal capsule. It has been shown by Franck and Pitres, and also by Minor,[3] that a current which causes no motor manifestation when applied to the nucleus caudatus causes active spasm when

[1] *Sur les Fonctions des Hémisphères Cérébraux.*

[2] Franck and Pitres, 'Sur les Convulsions Epileptiformes, &c.' *Archives de Physiologie*, 3me Série, Bd. ii.; Gliky, *Eckhard's Beiträge*, Bd. vii. 1876. This physiologist finds the corpus striatum inexcitable; but as his experiments were made on *sections* of the corpora striata they cannot be regarded as applicable to the ganglia in their normal condition.

[3] 'Ueber die Bedeutung des Corpus Striatum,' Abstract in *Neurolog. Centralblatt*, Bd. ii. 1883, p. 270.

applied direct to the internal capsule. Hence it is attempted to explain away the results of irritation of the nucleus caudatus by diffusion to the internal capsule. Minor further adduces in favour of this explanation the fact that in a dog on which some time previously he had extirpated the motor zone in one hemisphere, and so induced secondary degeneration in the internal capsule, no result was obtained on exposure and irritation of the nucleus caudatus. Irritation of the internal capsule was likewise without result—except closure of the opposite eye. The conclusion drawn from this and other experiments is that all the so-called effects of stimulation of the nucleus caudatus are really due to irritation of the internal capsule.

The arguments are an exact repetition of those which attribute the effects of irritation of the cortical centres to irritation of the subjacent medullary fibres. But though the internal capsule and the pyramidal fibres of the corona radiata are undoubtedly excitable, and continue excitable under conditions which annihilate all manifestations from stimulation applied to the centres, it by no means follows that the centres themselves are inexcitable. We have already seen that the intrinsic excitability of the cortical centres has been clearly established. The explanation of the phenomena of irritation of the nucleus caudatus by mere conduction to the internal capsule is disproved by the negative results of the same stimulus when applied to the optic thalamus. The motor tracts of the internal capsule are in point of fact closer to the optic thalamus than to the nucleus caudatus, and yet irritation of the optic thalamus causes no result. If it were merely a case of conduction to the motor tracts of the internal capsule electric stimulation of the optic thalamus ought to cause at least equal if not greater irritation of these tracts than electrisation of the nucleus caudatus. This, however, is not the case.

A mechanical excitability of a certain point in the nucleus caudatus, situated close to the third ventricle, has been contended for by Nothnagel,[1] who finds that in rabbits puncture

[1] Virchow's *Archiv*, Bd. lvii. 1873 *et seq.* He terms the spot the *nodus cursorius*—a term which stands on a par with his 'convulsion-centre,' previously referred to.

of this spot with a fine needle, or injection of a few drops of chromic acid, causes an apparently irresistible tendency on the part of the animal to run or jump till it becomes exhausted. As the phenomena he describes are merely the expression in the rabbit of some form of irritation, and not peculiar to irritation of the corpus striatum, no conclusions as to the special functions of this ganglion can safely be founded on them.

§ 4. It is one of the best established facts of human pathology that destructive lesions in the region of the corpus striatum cause hemiplegia of the opposite side of the body—a paralysis in general entirely confined to motion, sensation being in all respects unimpaired. Until recently no exact differentiation was attempted between the effects of lesions involving only the grey matter of the corpus striatum and those involving also, or alone, the anterior division of the internal capsule.

Since, however, it has been shown that the pyramidal tracts of the internal capsule have no relation, except that of contiguity, to the caudate or lenticular nucleus, it has become of importance to distinguish, if possible, between the effects of lesions of these parts respectively. As a rule, the lesions of disease are more or less indefinite, but the careful investigations of Charcot[1] and others have established that though lesions of the nucleus caudatus or nucleus lenticularis appear to cause hemiplegia, in all respects similar to that caused by lesion of the anterior two-thirds of the internal capsule, or of the cortical centres themselves, yet the hemiplegia depending on lesions limited to the grey matter of the striate nuclei is of a transitory character, and may entirely disappear even while the lesion remains. On the other hand, hemiplegia dependent on lesion of the fibres of the anterior division of the internal capsule is permanent, and is followed in due course by descending sclerosis of the pyramidal tracts and rigidity of the paralysed limbs.

Hence it would appear from the facts of human pathology that, provided the cortical motor centres and their pyramidal

[1] *Leçons sur les Localisations dans les Maladies du Cerveau*, 1876; Nothnagel, *Topische Diagnostik der Gehirnkrankheiten*, 1879.

tracts in the internal capsule remain intact, the ganglionic masses of the corpus striatum may be destroyed, or at least extensively injured, without giving rise to appreciable symptoms.

There are some facts which render it probable that lesions of the nucleus caudatus are more transitory in their effects than lesions of the lenticular nucleus. This would be in accordance with the anatomical researches, which seem to show that the fibres proceeding from the nucleus caudatus have to pass into the lenticular nucleus before reaching their peripherical destination.

The destruction of the nuclei of the corpus striatum, together with the related division of the internal capsule, does not appear to add to the effects of lesion of this division of the internal capsule by itself.

§ 5. Nothnagel[1] describes the results of a series of experiments on the basal ganglia of rabbits, in which he professes to be able to produce localised lesions of these structures by means of injections of chromic acid, or with the aid of a fine needle or trocar. The difficulties of exact localisation, however, are too great to allow of his results being accepted without question. It would appear, however, that, apart from the running or springing movements above referred to, mechanical lesions limited to the caudate nuclei caused little if any interference with volitional movements. Only in cases of unilateral lesion did there appear some impairment of movement and some deviation of the limbs. When both ganglia were extensively broken up no special symptoms were observable, even directly after the operation.[2]

Very different were the results of lesion of one or both lenticular nuclei. When one alone was destroyed by the injection of chromic acid, there occurred deviation outwards of the opposite fore limb, and deviation inwards of the hind limb of the same side, together with bending of the vertebral column towards the side of lesion, and some degree of cyphosis or dorsal curvature, due to paralysis of the contralateral trunk muscles.

[1] Virchow's *Archiv*, Bd. lvii., lviii., lx., lxii., 1873-1875.

[2] *Op. cit.* Bd. lx. p. 139.

When the lenticular nuclei were destroyed on both sides there was no deviation of the limbs or distortion of the trunk. The animals maintained their normal altitude, but remained quite immovable and apathetic, like animals deprived of their cerebral hemispheres. They allowed their limbs to be withdrawn or placed in any abnormal position without resistance. But if the tail were pinched the animal would make one or two leaps forward, and again relapse into its apathetic immobility.

Though Nothnagel assimilates the results of destruction of the lenticular nuclei to those observed after removal of the cerebral hemispheres, this is not strictly correct. Animals deprived of their cerebral hemispheres have neither desire nor the power of effecting volitional movements. But destruction of the lenticular nuclei paralyses only the power of carrying desire into effect. In a rabbit in which I had destroyed both corpora striata I observed clear indications of appetite and desire to eat; but attempts to satisfy them resulted only in vague and ineffectual struggles. Volitional movements only were paralysed, while perception, ideation, and desire continued—faculties which are entirely annihilated by complete removal of the hemispheres. It is a question whether the lesions described by Nothnagel were in reality confined to the respective ganglia of the corpus striatum, without implication of the internal capsule, directly or indirectly; but in any case it is evident that destruction of the ganglionic substance of the corpus striatum produces a much more complete and enduring paralysis than destruction of the cortical motor centres alone, or of the pyramidal tracts which proceed from them. The experiments of Carville and Duret [1] on dogs are in complete harmony with the results obtained in the case of rabbits. While removal of the cortical motor centres, or section of the pyramidal tracts before they penetrate between the nuclei of the corpus striatum, causes the characteristic paralysis or paresis already described and discussed, destruction of the corpus striatum with section of the pyramidal tracts forming the anterior division of the internal capsule (fig. 123), causes complete hemiplegia of the opposite side, so

[1] *Sur les Fonctions des Hémisphères Cérébraux.*

that the limbs are entirely useless either for support or progression. Here, too, as in rabbits, the hemiplegia, besides being much more complete than that resulting from destruction of the cortical motor area, appears to be much more enduring, if not permanent.

§ 6. In connection with lesions affecting the optic thalamus have been observed at one time paralysis of motion of the limbs generally, or of the upper limb in particular; at another, impairment or abolition of tactile sensibility or of vision; and in still other cases, considerable in number, no defect whatever, motor or sensory, has been apparent. It is altogether

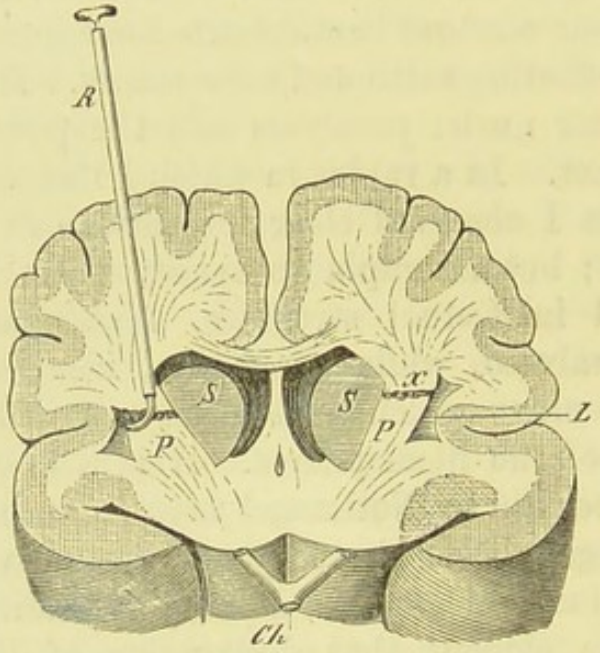


FIG. 123.—Frontal section of Brain of Dog, five millimetres anterior to the Optic Commissure (Carville and Duret). S S, nuclei caudati of the corpora striata. L, the lenticular nucleus. P P, the peduncular expansion. *Ch*, optic chiasma. *x*, section of the peduncular expansion causing *hemiplegia*. R, Veyssière's stylet for dividing the internal capsule.

impossible that lesions accurately restricted to the same region should have such a diverse symptomatology, and the negative cases are so numerous as to render very doubtful, if not absolutely disprove, any causal relationship between lesions of the optic thalamus as such and the sensory or motor symptoms which have been described in connection therewith.

It is easy to account for either sensory or motor paralysis in connection with lesions of the optic thalamus without attributing any special share in the causation to the thalamic grey matter itself. The position of the optic thalamus in

reference to the internal capsule is such (see fig. 25) that direct or indirect implication of its tracts must necessarily be always considered as possible, and indeed almost inevitable, if the lesion is at all extensive. It has been shown that many of the fibres of the internal capsule pass on to the cerebral cortex without entering into other relations than that of mere contiguity to the basal ganglia; and it has been found that section of the anterior two-thirds causes paralysis of motion, and lesion or section of the posterior third causes paralysis of sensation on the opposite side, both general and special.

It is necessary, therefore, to prove the absolute integrity of these tracts before we can ascribe either motor or sensory paralysis to lesions of the optic thalamus as such. The recorded cases by no means satisfy the requirements of scientific evidence in this respect, and the fact that not unfrequently lesions have been found in one or both optic thalami without discoverable symptoms goes far to prove that direct or indirect implication of the internal capsule has been the real cause in all cases where motor or sensory paralysis has been observed.

Though Luys[1] and Fournié[2] consider that the optic thalamus is the ganglion of convergence of all the sensory tracts before they radiate into the cerebral cortex, their views are neither in accordance with recent anatomical researches nor are they supported by well-established clinical or experimental data. The clinical cases collected by Luys in support of this theory are exceedingly unsatisfactory, and do not exclude implication of the internal capsule. The experiments which Fournié adduces to prove that destruction of the optic thalamus causes loss of sensation on the opposite side are not such as to inspire confidence. Fournié injected strong solutions of chloride of zinc into the optic thalami, but his own descriptions of the diffuse lesions, and general cerebral disturbance, which his procedure induced, justify the complete distrust with which his results have been received by physiologists[3] and pathologists in general.

[1] *The Brain and its Functions.*

[2] *Recherches Expérimentales sur le Fonctionnement du Cerveau*, 1873.

[3] See Nothnagel's trenchant criticism, Virchow's *Archiv*, Bd. lviii. p. 433.

Nothnagel[1] detected no paralysis either of motion or sensation after destruction of both optic thalami in rabbits, nor anything at first sight capable of distinguishing them from perfectly normal animals. They retained their voluntary motor power and reacted as usual to cutaneous stimulation. The only abnormality was that they allowed the fore limbs to be placed in any position without resistance, and if the one thalamus only were destroyed, the limb opposite the lesion. It is more than probable that this phenomenon depended on loss of sensibility of the limb, due to lesion of the internal capsule. For the mere reaction to cutaneous stimulation, which Nothnagel thinks sufficient to indicate the retention of tactile sensibility, is not a satisfactory proof of sensation. But Bechterew[2] did not observe this condition in his experiments, and saw nothing to indicate affection either of sensation or voluntary motor power. This author, however, states that electrical irritation of the optic thalamus in his hands caused the animals to utter cries such as they employ to express their feelings or emotions. I have, however, never observed any phenomenon of this nature in my experiments on the optic thalami of various animals, and cannot, therefore, admit the correctness of Bechterew's statements.

Bechterew further found that after destruction of the optic thalami in pigeons, fowls, rabbits, and dogs the animals were unable to express their feelings in the usual manner by cries, or to make the mimetic movements characteristic of feeling or emotion.

He admits, however, in a subsequent paper[3] that cries may still be elicited even after destruction of the optic thalami. These, however, he regards as merely reflex through the agency of 'elementary' centres in the pons or medulla, but true signs of feeling and true mimetic movements are only exhibited when the optic thalami are intact. Bechterew's criterion between reflex and true emotional cries and other manifestations of feeling appears to be somewhat arbitrary; and the experiments of Longet and Vulpian, as well as my

[1] Virchow's *Archiv*, Bd. lxii.

[2] 'Die Function der Sehhügel,' *Neurolog. Centralblatt*, No. 4, 1883.

[3] *Neurolog. Centralblatt*, No. 4, 1884.

own, previously described (Chapter V.), are distinctly contradictory in several particulars of the results arrived at by him.

Whatever may be the special results of destruction of the optic thalami, it seems fairly well established by the facts of disease, and experiments on the lower animals, that they may be extensively destroyed, if not entirely extirpated, without causing paralysis of voluntary motion or loss of tactile sensation. When these symptoms occur in connection with lesions in the region of the optic thalamus, they may with more reason be ascribed to injury of the internal capsule than to the lesion of the optic thalamus as such.

§ 7. It is a question, however, whether the optic thalamus has not a special relation to vision. As has been seen, one of the roots of the optic tract is traceable to the external geniculate body and pulvinar of the optic thalamus, and other fibres have been described as arising from the superficial stratum, as well as from the interior of this ganglion. There are clinical as well as experimental facts to show that lesions invading the posterior region of the optic thalamus cause homonymous hemiopia by paralysis of the corresponding side of both retinæ. Thus in a case reported by Hughlings Jackson [1] in which there was softening in the region of the pulvinar of the right optic thalamus, and apparently limited to this region, there was observed during life left hemiopia from paralysis of the right side of both retinæ. But as, in addition to the hemiopia, there was also some defect in motor power, as well as some impairment of general sensibility on the left side, there is every reason for believing that the posterior division of the internal capsule was also more or less directly or indirectly implicated. Other similar cases might be alluded to. But, even though we may admit that lesions accurately restricted to the pulvinar and corpora geniculata may cause hemiopia, this may be ascribed merely to interruption of the optic radiations which proceed from this part towards the occipito-angular region of the hemisphere. We have seen that hemiopia may be induced by cortical and subcortical lesion of the occipito-angular region. The question is whether there is anything to distinguish hemiopia so induced from that caused

[1] 'A Physician's Notes on Ophthalmology,' *Lond. Hosp. Reports*, 1875.

by lesion limited to the pulvino-geniculate region of the optic thalamus itself. In an experiment which I made on a monkey, in which the left optic thalamus, along with the medullary fibres external to it, was extensively broken up by penetration from the cortex in the region of the first occipito-angular bridging convolution (fig. 124), there was, in addition to general hemianæsthesia, total blindness of the opposite eye—temporary at least, but whether giving place to homonymous hemiopia was not determined—and also dilatation of the opposite pupil. As dilatation of the pupil does not occur in cortical or subcortical lesion of the occipito-angular region, this symptom may possibly be a special feature of lesion of the optic tract in the thalamus itself; indicative of rupture of the centripetal

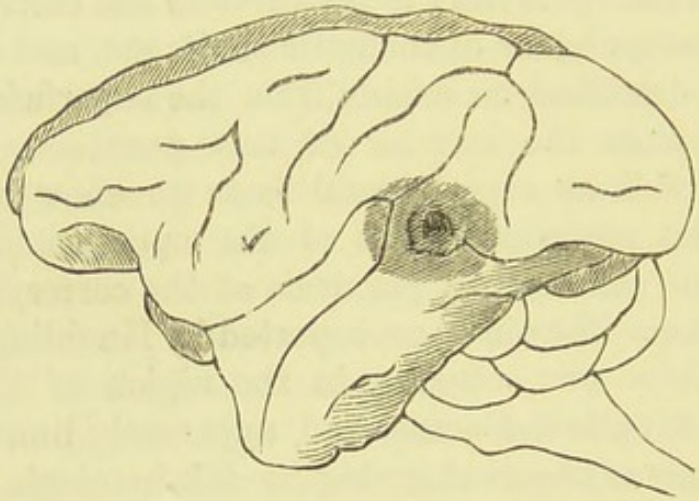


FIG. 124.—The shading indicates the superficial extent of the lesion in the left hemisphere in the operation for destruction of the optic thalamus. The darker centre indicates the sinus leading into the optic thalamus.

fibres to the irido-motor nucleus in the floor of the Sylvian aqueduct.

§ 8. An analysis of the various clinical and experimental data in reference to the effects of lesions of the ganglionic substance of the corpora striata and optic thalami leads to the conclusion that, provided the fibres of the internal capsule are not directly or indirectly injured, neither voluntary motion nor sensation is permanently impaired or abolished. For we cannot consider that Nothnagel's experiments on the lenticular nucleus exclude implication of the internal capsule; inasmuch as not in every case, but only in those in which the lesion penetrated deeply, as far as the base of the ganglion, was

voluntary motion paralysed. Lesions of small size and situated well outwards from the internal capsule had no such effect. And the probability is that in all successful cases the internal capsule was really injured directly or indirectly.

But it is not difficult to discover, in certain animals at least, a very great difference between the effects of destruction of the cortical motor centres or of the subjacent medullary fibres, and those following destruction of the ganglia of the corpus striatum, together with the tracts of the internal capsule passing through them. The degree of motor paralysis from lesion of the striate-capsular region in different animals appears to bear an inverse ratio to that resulting from purely cortical or subcortical lesion of the motor zone.

In man and the monkey there is little if any difference between the effects of complete destruction of the cortical motor centres and those of destruction of the striate-capsular region. There is the same powerlessness of the opposite side of the body, and the same lateral distortion from the unantagonised action of the muscles on the sound side. The degree of paralysis of the various movements corresponds, those movements being most affected which are the most complex, most volitional, and most independent; and the duration of the paralysis is, as far as can be judged, as lasting in the one case as in the other, and followed by the same secondary degeneration of the pyramidal tracts of the spinal cord. But while complete hemiplegia of the opposite side can be produced by a very limited lesion in the striate-capsular region, the same effect can only result from a very extensive lesion of the cortex. Hence it is more rare to find complete hemiplegia from cortical lesion than from lesion in the region of the corpus striatum. Only those movements are permanently paralysed the cortical centres of which are thoroughly disorganised; while others which have their centres only slightly injured, or merely functionally affected, are recovered when the causes of the perturbation have completely subsided.

In dogs, however, as the experiments of Carville and Duret prove, destruction of the striate-capsular region produces a much more complete paralysis than lesion of the cortex or subjacent fibres. In the latter case the affection of motility

is so slight that it has been described as a paresis rather than a paralysis, and the animal is able to perform many actions apparently as well as before. But in the former case complete hemiplegia is the result. The limbs are entirely powerless, and lateral distortion of the trunk towards the side of lesion occurs. The animal is unable to stand or walk, or if it attempts to move it is impelled to move round in a circle by the action of the unparalysed side.

In rabbits, on the other hand, the destruction of the cortical motor centres produces much less marked disturbance of the ordinary motor activities than even in dogs. But when the corpora striata and corresponding division of the internal capsule are destroyed there is complete paralysis of voluntary motion, and only those movements are possible which are capable of being carried out through the cerebellar, mesencephalic, and spinal centres in the entire absence of the cerebral hemispheres.

These differences in the effects of destruction of the cortical motor centres and corpora striata in the different orders of animals, throw considerable light on the special functions of these ganglia. In the rabbit the powers of equilibration and co-ordinated locomotion are not abolished either by destruction of the corpora striata or cortical centres, or both together. In the dog the destruction of the corpora striata (including the corresponding division of the internal capsule) causes complete paralysis (for the time at least) of all the powers of movement which are only partially affected by removal of the cortical centres ; while in the monkey and man the destruction of the corpora striata adds little or nothing to the completeness of the motor paralysis which results from destruction of the cortical motor centres.

These differences can only be satisfactorily accounted for on the principles already repeatedly enunciated—that animals differ greatly in respect to the degree of organisation of the ordinary motor activities in the lower centres. This is much greater in the lower than the higher vertebrates, as is shown by the results of complete ablation of the cerebral hemispheres ; and it is evident that the independent organisation of the motor activities in the mesencephalic and lower ganglia is

much greater in the rabbit than in the dog. For even when the corpora striata and corresponding division of the internal capsules are disorganised in the rabbit, equilibration and co-ordinated locomotion are still possible in response to appropriate external stimuli; whereas in the dog there is such complete powerlessness that the animal lies perfectly helpless, unable to stand or walk.

It appears from these facts that the corpora striata proper are centres of innervation of the same movements as are differentiated in the cortical motor centres, but of a lower grade of specialisation. The innervation of the limbs in all that relates to their employment as instruments of consciously discriminated acts is dependent on the cortical centres, while for all other purposes involving mere strength or automatism, primary or secondary, the corpora striata with the lower ganglia are sufficient. In man almost every movement has to be laboriously acquired by conscious effort through the agency of the cortical centres, and continues to involve the activity of these centres to a greater or less extent throughout. Hence the destruction of the ganglia of the corpora striata adds little if anything to the completeness of the paralysis which results from destruction of the cortical motor centres alone.

§ 9. As to the special functions of the optic thalami, so far as any definite facts have been ascertained, apart from mere hypotheses more or less plausible, we may still say with Vulpian, 'Nous ne savons rien des fonctions spéciales des couches optiques.'[1] In the absence of any definite symptoms resulting from destruction of these ganglia, apart from such as may with more probability be ascribed to coincident lesions of the internal capsule or optic tracts, we can only speculate as to their proper functions.

If the anatomical relations were more satisfactorily determined than they are in reality, we might found more securely on these than we can safely do as yet. But it seems at least certain that they have a closer relation to the sensory tracts and centres than they have to the motor. The cutaneous sensory tracts of the internal capsule are immediately in relation to them, and indeed Flechsig, as we have seen, traces

[1] *Leçons*, &c. p. 659.

them all, though in all probability erroneously, entirely into the tegmentum, with which the optic thalamus is more or less directly continuous. The optic tracts, besides other supposed connections with the optic thalami, are certainly connected with the pulvino-geniculate region of these ganglia. By the pillars of the fornix the optic thalami are in relation with the cortical centres of smell (taste?) and tactile sensibility. Through the fibres of the corona radiata they are in relation with the occipito-temporal regions of the cortex, which, we have seen, are sensory in function. The anterior tracts appear to pass into the frontal regions, but where they end has not been

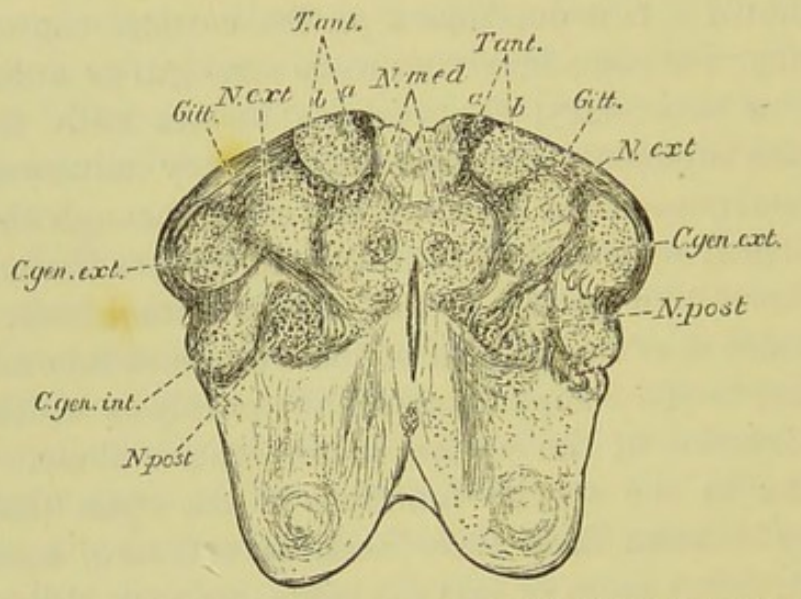


FIG. 125.—Horizontal Section of the Optic Thalami of Rabbit, just above the level of the internal capsule (after Monakow). *T.ant.*, tuberculum anterius. *a*, anterior, and *b*, posterior cell group of the same. *N.med.*, median nucleus. *N.ext.*, external nucleus. *N.post.*, posterior nucleus of the optic thalamus. *Gitt.*, cancellated layer (Gitterschicht). *C.gen.ext.*, corpus geniculatum externum. *C.gen.int.*, corpus geniculatum internum.

satisfactorily determined, and it is not improbable that they enter the gyrus fornicatus.

Monakow's experiments lead him to conclude that each nucleus of the optic thalamus (fig. 125) is related to a definite cortical region, and undergoes atrophy with its related tracts when this region is extirpated. Thus he concludes that the posterior nucleus (fig. 125, *N.post.*) is specially related to the basal regions of the hemisphere; the pulvinar and corpus geniculatum externum (fig. 125, *C.gen.ext.*) to the occipital region or visual sphere; the corpus geniculatum internum (fig. 125,

C.gen.int.) to the temporal region or auditory zone; the external nucleus (fig. 125, *N.ext.*) and neighbouring parts to the upper and lower parietal regions; and the anterior tubercle and median nucleus (fig. 125, *T.ant.*, *N.med.*) to the frontal regions of the hemisphere. In addition to the nuclei of the optic thalamus the correlated medullary fibres of the corona radiata, and also the tracts leading to the periphery, undergo atrophy, particularly—apart from the pyramidal tracts related to the motor zone—those of the outer part of the crus and those passing into the tegmentum. The course of these latter fibres is uncertain. But apparently there ensues atrophy to some extent in the formatio reticularis, the middle cerebellar peduncle, the trapezium and lateral portion of the lemniscus of the same side, and the opposite half of the spinal cord.

Before these results can be accepted as correct it will be necessary to repeat the experiments in such a manner as to ensure absolute limitation of the primary lesions, conditions far from being fulfilled by Monakow's researches, and it will be necessary also clearly to differentiate lesions implicating the falciform lobe from those of the convexity. There is reason to believe that the relations which he seeks to establish between lesions of the frontal regions and the anterior tubercle are founded on implication of the gyrus fornicatus.

Gudden[1] did not observe any abnormality in the appearance of the optic thalamus after extirpation of the motor zone, which caused degeneration of the pyramidal tracts. Nor did Monakow in his first experiments note any atrophy of the optic thalamus after destruction of the frontal region, though his subsequent researches led him to a different conclusion. That the optic thalamus is at all related to the true motor zone is extremely doubtful. In a remarkable case reported by myself,[2] in which the whole of the motor zone with the exception of the marginal convolution and portion of the postero-parietal lobule was entirely atrophied—a condition which had existed many years—the optic thalamus with the exception of the anterior tubercle, which was destroyed along

[1] *Archiv für Psychiatrie*, Bd. ii. 1871.

[2] See figs. 64, 65, Chap. VI. p. 216.

with the corpus striatum by the primary lesion, was perfectly normal in size and appearance as compared with that of the other side.

So far as has yet been established beyond doubt the optic thalamus appears to be related to sensory regions and tracts, and more especially has this been demonstrated of the visual sphere.

§ 10. It is, however, evident from the results of experiment and disease that the centres of the optic thalamus are not the centres of 'conscious' sensation, nor are the paths which connect them with the cortex the paths, or at least the only paths, of sensation; inasmuch as it is only when the posterior portion of the internal capsule is destroyed that anæsthesia results, and this apparently without any evident implication of the ganglionic substance itself. There are no facts or data serving to define with any degree of definiteness the functions of the respective nuclei and their correlated tracts in the corona radiata. The tracts may be the paths of obscure sensations, some of which may be perhaps related to the organic sensibilities, or they may be merely tracts of association between the centres of conscious and subconscious activity. It is probable that the optic thalami, specially related to the sensory tracts, and the corpora striata, specially related to the motor tracts, represent in a subordinate manner all the sensory and motor centres of the cortex, and constitute together a sensori-motor mechanism, subservient to the manifestation of all those forms of activity which do not imply conscious discrimination or true volition.

In proportion as the capacities and modes of activity transcend mere consensual or adaptive automatism, and involve conscious discrimination and special motor acquisition, do the cortical centres become necessary, as in man. In such case the basal ganglia may be more or less completely dispensed with, as would appear from the absence of permanent symptoms in case of lesions confined to the ganglionic substance proper. If, on the other hand, as in rabbits, the modes of activity do not greatly transcend mere automatism, the cortical centres are of less importance, and may be removed without creating much obvious disturbance.

In intermediate cases, as in dogs, the degree of disturbance caused by removal of the cortical centres will depend on the relative proportion in their modes of activity between mere automatism, provided for by the basal ganglia, and special acquisitions which have involved the exercise of conscious discrimination.

CHAPTER XII.

THE HEMISPHERES CONSIDERED PSYCHOLOGICALLY.

§ 1. HITHERTO we have considered the brain chiefly in its physiological aspects, and the conclusion has been arrived at that the hemispheres consist of a system of sensory and motor centres. In their subjective aspect the functions of the brain are synonymous with mental operations, the consideration of which belongs to the science of psychology. The phenomena of consciousness cannot be investigated or explained by physiological methods only, but anatomical and physiological investigation of the substrata of consciousness may serve to elucidate some at least of the correlations between conditions of the brain and psychical manifestations. It is not the object of this chapter to attempt an analysis of mind or the laws of mental operations, but briefly to discuss, in the light of the facts revealed by the physiological and pathological researches recorded in the preceding chapters, some of those relations between the physiological and psychological functions of the brain which present themselves more especially to the physician and medical psychologist.

That the brain is the organ of the mind is a universally admitted axiom. We have no proof of subjectivity or modifications of consciousness apart from the action of the cerebral hemispheres. But we have no reason to believe that anything is superadded, or that the action of the cortical centres is of a different order from that of the most simple nervous apparatus; but rather that between the simplest reflex action and the most complex cerebral process there is a continuous unbroken gradation. Why consciousness should arise only in correlation with the activity of the cerebral hemispheres is a question which has not yet received any satisfactory answer.

It may perhaps be associated with greater complexity or friction than obtains in lower ganglia; but though we should arrive at the true explanation of the conditions of consciousness when a sensation is experienced, we are as far as ever from understanding the ultimate nature of that which constitutes the sensation. The one is objective and the other subjective, and neither can be expressed in terms of the other. We cannot say that they are identical, or that one passes into, or causes the other; but only, as Laycock expresses it, that the two are correlated; or, with Bain, that the physical changes and the psychical modifications are the objective and subjective sides of a 'double-faced unity.' 'We have every reason for believing that there is, in company with all our mental processes, *an unbroken material succession*. From the ingress of a sensation to the outgoing responses in action the mental succession is not for an instant dissevered from a physical succession. A new prospect bursts upon the view; there is a mental result of sensation, emotion, thought, terminating in outward displays of speech or gesture. Parallel to this mental series is the physical series of facts, the successive agitation of the physical organs. . . . While we go the round of the mental circle of sensation, emotion, and thought there is an unbroken physical circle of effects. It would be incompatible with everything we know of cerebral action to suppose that the physical chain ends abruptly in a physical void, occupied by an immaterial substance; which immaterial substance, after working alone, imparts its results to the other edge of the physical break, and determines the active response —two shores of the material with an intervening ocean of the immaterial. There is, in fact, no rupture of nervous continuity. The only tenable supposition is that mental and physical proceed together as undivided twins. When, therefore, we speak of a mental cause, a mental agency, we have always a *two-sided cause*; the effect produced is not the effect of mind alone, but of mind in company with body.' [1]

In accordance with this position it must follow, from the constitution of the cerebral hemispheres, that mental operations in the last analysis must be merely the subjective side

[1] Bain, *Mind and Body*, 1873, p. 131.

of sensory and motor substrata, as has been clearly enunciated by Hughlings Jackson. For the cerebral hemispheres consist only of centres related respectively to the sensory and motor tracts, which connect them with the periphery and with each other.

§ 2. The physiological and psychological activity of the cerebral hemispheres are not, however, altogether coextensive. While consciousness cannot arise apart from the activity of the hemispheres, many cerebral processes can occur without revealing themselves in consciousness.

The brain as an organ of motion and sensation, or presentative consciousness, is a single organ composed of two halves; the brain as an organ of ideation, or re-presentative consciousness, is a dual organ, each hemisphere complete in itself. When one hemisphere is removed or destroyed by disease, motion and sensation are abolished unilaterally, but mental operations are still capable of being carried on in their completeness through the agency of the one hemisphere. The individual who is paralysed as to sensation and motion by disease of the opposite side of the brain (say the right) is not paralysed mentally, for he can still feel and will and think, and intelligently comprehend with the one hemisphere. If these functions are not carried on with the same vigour as before, they at least do not appear to suffer in respect of completeness.

§ 3. In order that impressions made on the individual organs of sense shall excite the subjective modification called a sensation, it is necessary that they reach and induce certain molecular changes in the cells of their respective cortical centres.

If the visual centre is destroyed or functionally inactive, impressions made on the retina and optical apparatus cause the same physical modifications as usual, but do not affect consciousness. The changes produced have no subjective side.

The optical apparatus without the visual centre may be compared to the camera without the sensitised plate. The rays of light are focussed as usual, but produce no chemical action, and leave no trace when the object is withdrawn, or the light from it shut off. The visual centre is like the sensi-

tive plate. The cells undergo certain molecular modifications which coincide with certain subjective changes constituting the consciousness of the impression or special visual sensation. And as the sensitive plate records, in certain chemical decompositions, the form of the object presented to the camera, so the visual centre records in cell-modifications the visual characters of the object looked at. We may push the analogy still further. Just as the chemical decomposition effected by the rays of light may be fixed and form a permanent image of the object capable of being looked at, so the cell-modifications which coincided with the presentation of the object to the eye remain permanently, constituting the organic memory of the object itself. When the same cell-modifications are again excited, the object is re-presented or rises up in idea. It is not meant by this analogy that the objects are photographed in the visual centre, as objects are photographed on the plate, but merely that permanent cell-modifications are induced, which are the physiological representatives of the optical characters of the object presented to the eye. The optical characters are purely light vibrations, and few objects are known by these alone. The object appeals to other senses, and perhaps to movements, and the idea of the object as a whole is the revival of the cell-modifications in each of the centres concerned in the act of cognition. For what is true of the visual centre is true, *mutatis mutandis*, of the other sensory centres. Each is the substratum of consciousness of its own special sensory impressions, and each is the organic basis of the memory of such impressions in the form of certain cell-modifications, the re-induction of which is the representation or revival in idea of the individual sensory characters of the object. The organic cohesion of these elements by association renders it possible for the re-excitation of the one set of characters to recall the whole.

§ 4. The sensory centres, therefore, are to be regarded not merely as the organs of consciousness of immediate sensory impressions, but as the organic register of their own sensory experiences. This organic memory is the physical basis of Retentiveness, and the property of re-excitability is the organic basis of Recollection and Ideation. We have thus a physio-

logical foundation of the law arrived at on other grounds by Bain, viz. that 'the renewed feeling occupies the very same parts, and in the same manner as the original feeling.' According to Spencer, the renewal of the feeling is the *faint* revivification of the same processes which are *strongly* excited by presentation of the object. The molecular thrill, if we may so term it, of present sensation extending from the peripherical organ of sense is in the ideal sensation revived, but, as a rule, not so powerfully as to extend to the periphery; though, in some instances, the central revivification may be so intense as actually to reinduce the peripherical impression. This occurs in certain morbid states, such as are described under the name of 'fixed ideas,' or in sensory hallucinations from diseased conditions of the brain, as in epilepsy and insanity.

The organic memory of sensory impressions is the fundamental basis of knowledge. If the sense impressions were evanescent, or endured only so long as the object was present, the range of conscious intelligent action would be limited to the present, and we should have no real knowledge. Knowledge implies the consciousness of agreement or difference. We can only be said to *know* when we recognise identity, or difference between past and present conscious modifications. We know that a certain colour is green by recognising a similarity or identity between the present and a certain past colour sensation, or a difference between this and some other colour in the spectrum. If we had no organic memory of the past capable of re-excitation to serve as the basis of comparison, we should be unable to recognise either agreement or difference. We might be conscious from moment to moment, but there would be no continuation in time, and knowledge would be impossible. The foundation of the consciousness of agreement is the re-excitation by the present of the same molecular processes which coincided with a past impression; and of difference, a transition from one physical modification to another. The sensory centres, therefore, besides being the organs of sensation or consciousness of immediate impressions, contain, in the persistence and revivability of the coincident physical modifications, the materials and possibilities of simple

and complex cognitions, in so far as these are dependent on sensory experience alone.

The destruction[1] of the visual centre, therefore, not only makes the individual blind presentatively, but blind re-presentatively[2] or ideally, and all cognitions into which visual characters enter in part or whole become mangled or imperfect, or are utterly rooted out of consciousness. The destruction of the eye renders the individual blind only presentatively, but his visual memory and visual ideation remain unaffected;[3] and it would be of great importance to ascertain whether in an individual born blind, or blind for many years, the visual centres, apart from mere general atrophy, present any special peculiarities in the appearance of the cells or their processes differing from those of the normal brain.

§ 5. The springs of conscious activity, or the incentives to volition, are present or ideally revived sensations and their accompaniments. Sensations are accompanied in consciousness by feelings, which are divisible into two great and opposite classes, pains and pleasures. Just as sensations are the subjective side of certain physical modifications of the nerves and nerve centres, so pleasurable or painful feelings may be regarded as the subjective expression of physical harmony or disharmony between the organism and the influences acting on it. A painful sensation is a physiological discord incompatible with health or comfort, or, it may be, life itself. A pleasurable sensation is a physiological harmony promoting health and comfort, and calculated to prolong existence.[4]

[1] See further on this subject, § 14.

[2] The distinction here drawn between presentative and re-presentative blindness and other states of consciousness, long familiar to English psychologists, has been travestied by Munk under the terms 'cortical blindness' (Rindenblindheit) and 'psychical blindness' (Seelenblindheit). As all the manifestations of cerebral action, objective and subjective, are at bottom cortical, it is manifestly absurd to establish an antithesis between 'cortical' and any other form of blindness.

[3] This is not strictly accurate except within certain limits. There is reason to believe that, unless the centres are kept in exercise by the continuous incoming of new impressions, they tend to degenerate, so that former sensory experience is lost or cannot be revived. It is well known that when total deafness occurs in early life dumbness ensues, even though the child may have learnt to talk with fluency.

[4] As Romanes (*Mental Evolution in Animals*, p. 107) truly remarks, 'the

As the revived or ideal sensation involves the activity of the same structures as are concerned in the present sensation, so the revived feelings or emotions are localised in the same regions. Hence the sensory, ideational, and emotional centres are one and the same. The senses differ greatly in respect to the relative preponderance of the intellectual or discriminative, and emotional, or feeling, element in their composition, and in respect to their revivability as ideas or as feelings. In the visual sense the emotional is subordinate to the intellectual, or may be almost entirely absent, and in the great majority requires cultivation; in the sensations of organic life the emotional is at its maximum, and the intellectual or discriminative at its minimum. In man vision is the highest intellectual sense, while smell and taste are the highest in point of feeling. In dogs and other animals, however, this rule does not seem to obtain, and smell appears to rank higher than the other senses in an intellectual point of view. The manner in which dogs, with their extraordinary keenness of smell, are able to investigate with their olfactory organs substances which to man, with his feebly developed sense of smell, would be the cause only of the most unpleasant feelings, shows that the sense of smell in them is largely dissociated from mere feeling, and is the chief organ of intellectual discrimination.

The feelings accompanying the more intellectual senses, vision and hearing, are the primordial elements of the æsthetic emotions which are founded on harmonies of sight and sound. All the emotions, however complex or difficult of analysis, are founded ultimately on the feelings accompanying the exercise of the centres and organs of sensation. That the sensations of organic life are represented in the cerebral hemispheres, directly or indirectly, is plain from the extraordinary influence which states of the viscera exercise on the emotional tone of the individual. Organic sensations generally, with

superficial or apparent objection to the doctrine we are considering, which arises from the fact that feelings of pleasure or pain are not infallible indices of what is respectively beneficial or injurious to the organism, is easily met by the consideration that in all such exceptional cases it is not the doctrine, but its application, which is at fault.'

one or two exceptions, are, unless rising to the pitch of painful intensity, obscure and non-localisable, and the healthy or morbid physiological activity is expressed subjectively as the vague and ill-defined feeling of well- or ill-being—*euphoria* or *dysphoria* (Laycock). Whether the centres of organic sensation are fused with those of tactile or common sensibility in the falciform lobe, or whether they are specially represented in and through the optic thalami or elsewhere are all questions as yet unsolved. But, wherever situated, they seem to be the foundation or universal background of pleasurable or painful emotions in general. As healthy states of the viscera produce pleasurable feelings, and morbid states of the viscera produce painful or depressing feelings, so, conversely, on the principle that the revived feeling occupies the same parts as the original, pleasurable emotions exalt, and painful emotions depress, the vital functions. Visceral derangements are frequently the cause, and always the accompaniment, of melancholic depression; and just as visceral derangements frequently express themselves in localisable sympathetic neuroses, so the melancholic individual, or hypochondriac, projects his obscure feelings in some definite objective form. He imagines that his vitals are being gnawed at by some hideous animal, or that his body is the scene of demoniacal revels. The special form of the hallucination varies with the individual and his education, but it always takes some dread or malignant shape.

§ 6. The physiological needs of the organism in so far as they induce locally discriminable sensations express themselves subjectively as definite appetites or desires, which are the conscious correlations of physiological wants. The appetite of hunger is the desire to satisfy or remove a local sensation, referable to the stomach, in which the physiological needs of the organism express themselves. The substrata of the feeling of hunger and appetite for food are the stomachic branches of the vagus and their cerebral centres. And as local conditions of the stomach may destroy or increase the feeling of hunger, so central disease may give rise to ravenous appetite or sito-phobia, conditions exemplified in certain forms of insanity.

The bodily need of water expresses itself locally in a dry condition of the fauces, which is the basis of the feeling of thirst and the appetite for drink.

The sexual appetite, though springing from the organic wants of certain glandular structures, centres itself round a certain tactile sensation, which is the reflex key to the gratification of the physiological demand for functional exercise on the part of these organs. The sexual appetite appears only with the development of the generative glands. Its appearance induces considerable perturbation of the other organic functions, and expresses itself subjectively at first chiefly in the form of emotional excitability, or in obscure longings, morbid desires, or hysterical outbursts. Long before the link between a definite sensation and a definite action for its realisation has been established in consciousness, the generative glands may gratify themselves reflexly during sleep, the period, *par excellence*, of reflex excitability. As morbid irritation of the generative organs may excite a morbid sexual appetite, so, conversely, the sexual appetite may be morbidly excited by pathological irritation of the cerebral paths and cerebral centres of the sensations connected with the exercise of the generative functions. To the former belong the satyriasis or nymphomania occasionally observed in connection with disease of the middle lobe of the cerebellum; to the latter the various morbid exhibitions of the sexual appetite in insanity where the centres are functionally or organically diseased.

§ 7. The various sensations, feelings, and desires, present or revived, singly or in associated combinations, form the incentives to action, the motives to volition.

The outward expression of certain physiologically hurtful or beneficial sensory impressions takes place instinctively or independently of individual education; their realisation in consciousness, as painful or pleasurable sensations, merely coinciding with, or, in strict accuracy, more often following, their manifestation externally. Such are the spinal reflex actions, and the reflex expressions of emotion such as we have seen manifested in animals deprived of their cerebral hemispheres.

All truly volitional action, on the other hand, is the result

of education, the duration of which varies within extremely wide limits in different classes and orders of animals, and in respect to individual acts of volition in the same animal.

At birth the human and monkey infant have no volition proper, but only the elements out of which it is evolved. The actions of the infant are at first limited to definite reflex response to definite external or internal stimuli, and to indefinite or general motor activity, conditioned not so much by any definite stimulus as by a natural tendency of the nerve centres to expend their surplus energy in action. To this latter tendency Bain gives the name 'spontaneity.' Though it is impossible to determine how far this expenditure of energy is dependent on central overflow alone, and how far on external and internal sensory impressions in general acting on the nerve centres, the term spontaneity sufficiently well expresses a definite fact of the constitution.

Actions determined reflexly, or originating spontaneously, according as they prove physiologically beneficial and subjectively pleasurable, tend to continuance and repetition; while actions physiologically hurtful and subjectively painful are checked or avoided. This is the great law of self-conservation, exemplified in the struggle for existence and the survival of the fittest. It is only in accordance with this law that animals have been able to adapt themselves to their environment, and those have succeeded best in which the internal adaptations have best corresponded with its provisions.

The conscious discrimination of a sensation as pleasurable, and its ideal persistence and tendency towards repetition as desire, and its association with things seen, smelt, or tasted, are effected long before the sensation, present or revived, is associated with any differentiated motor act for its accomplishment or realisation. This latter is the result of happy accident, or of repeated trials and error. Though the child possesses in the motor centres[1] of its cerebral hemispheres the potentiality of differentiated motor acts, the individual selection or excitation, of any one of these, in response to a present or revived sensation, requires the establishment, by

[1] These, according to the experiments of Soltmann on dogs, already alluded to (p. 234), are not developed so as to be excitable in the earlier days of infancy.

education and repetition, of an organic nexus between the special sensory centre or centres, and the special motor centre. Some particular object held before a child recalls by sight a pleasurable sensation, and excites desire; but, instead of inducing, as yet, a definite action for its gratification, excites only vague and undefined movements of arms, legs, and facial muscles, the expression of general excitation of the motor centres. In process of time the centre of the special differentiated movement necessary to the gratification of the desire can be thrown individually into action, and thus a definite act of volition is, for the first time, fairly accomplished.

Voluntary control is first established over those movements which are also most easily called into play by reflex stimulation. A child can voluntarily grasp with its fist long before it can raise its hand to its mouth, or put out its hand to lay hold of anything. This is parallel with the fact that the hand can be made to close reflexly over any object placed in the palm, long before the same action can be performed voluntarily. And it is curious and interesting to observe in a child, how, in the growth of volition, the first action fairly differentiated in response to any particular sensation or desire is repeated in response to desire in general, however ludicrously insufficient to accomplish the desired end. The individual activity of the various specially differentiated motor centres having once been fairly established, at first in response to particular sensations and desires, voluntary acquisition proceeds apace, the centres being free to form new associations and become the means of realisation in action of all the varied simple and complex impulses of the sensory centres. The associating fibres between the one motor centre and the various sensory centres may thus become innumerable.

The rate at which the organic nexuses are established between the sensory and motor centres varies according to the degree of complexity and intricacy of the movements. Complex and intricate movements are longer in being acquired than those which are simple, and also reflex or already hereditarily organised. Hence the movements of articulation in combination with those of vocalisation are longer in being acquired than those of the arms or legs.

In the lower animals the control and co-ordination of movements are almost complete at birth, or require little education as compared with the prolonged helplessness of the human infant.

Some birds start from the egg already fully equipped, like Athene from the head of Zeus. They are in great measure mere 'conscious automata.' They are capable of acquiring sensory experience and association of ideas, but of little further motor acquisition beyond that with which they start in life. Their cortical motor centres count for little, and may be removed without causing much disturbance of their ordinary modes of activity. Rabbits require but comparatively short education to perfect their powers; cats and dogs longer; but cats and dogs are already advanced in life, and have assumed the cares of paternity, or rather maternity, when the human infant can scarcely lift a finger in its own behalf.

In proportion as volition predominates over conscious automatism, is education necessary to perfect the powers of movement; in the same proportion are the cortical motor centres developed; and in that proportion are the powers of movement paralysed by destruction of the motor centres of the hemispheres.

In the rabbit conscious automatism is more marked than in the dog; the period of education is shorter; the faculty of further special motor acquisition is small, the cortical centres are but lowly developed; and their removal exercises but slight and transient disturbance of their ordinary modes of action. In the dog volition enters more largely into the motor activities; the period of education is longer; the faculty of special motor acquisition beyond the mere power of locomotion is greater; the cortical motor centres are more highly developed, and their removal causes greater disturbance of their motor powers, not however permanently paralysing their conscious-automaticity, but abolishing their special voluntary motor acquisitions. In man volition is predominant; education is long and laborious; the faculty of special motor acquisition is unlimited; the cortical motor centres reach their highest development; and their removal causes such complete and enduring motor paralysis as to indicate that

automatism in and by itself is scarcely detachable from the centres of consciousness and volition.

§ 8. Man is not merely a passive or receptive organism capable of perceiving and registering impressions made on his organs of sense, but also an active, or executive, organism possessing organs of the most varied and complex motor achievements. In the same manner as the sensory centres are the organs of special sensory perception and the organic basis of the memory of sensory impressions, so the motor centres of the cortex, besides being the organs of differentiated movements, are the organic basis of motor acquisitions. But while the activity of the sensory centres reveals itself subjectively in consciousness as ideation or feeling, the activity of the motor centres has no subjective side apart from the functioning of the sensory centres, with which they are associated. Modifications of consciousness are correlated exclusively with the functioning of the sensory centres of the cortex.

We have therefore in the cortex centres of sensation and centres of motion, centres of sensory and centres of motor acquisition or registration, an organic sensory and an organic motor memory ; but whereas we have sensory ideation in and by itself, we have no ideas of movement apart from the sensory centres through which alone the activity of the motor centres is revealed in consciousness.

The motor activities called into play by definite feelings and sensations, present or revived, constitute volitional movements, and the organic cohesion formed between the sensory and motor centres, persistently enduring in these centres, is the physical basis of our intellectual and volitional acquisitions in all their manifold range and complexity. The motor centres and motor faculties, besides furnishing the conditions and possibilities of multiple and varied voluntary movements, and the organic registration of these as motor or mechanical acquisitions, enormously widen the field of sensory experience and complicate its results. By the movements of the head and eyes we greatly extend the scope and complicate the facts of visual sensation, and by the movements of the limbs the range of tactile experience is increased a thousandfold.

There are few objects of cognition known to us only by

passive sensory characters or impressions. The vast majority involve the activity both of our sensory and motor faculties, and our ideas are a mixed revival both of movements and sensations in their respective coherent associations. This is exemplified in the acquisition and constitution of ideas of form, shape, weight, resistance, and the like.

Our ideas of form are not mere revived optical impressions, which are properly limited to colour (except perhaps in so far as the object viewed does not subtend a visual angle larger than can be included easily within the punctum centrale retinæ), but optical impressions combined with ideal ocular movements. Our idea of a circle is a combination of an ideal coloured outline with an ideal circular sweep of the eyeballs, or, it may be, of the tactile impressions coinciding with an ideal circumduction of the arm or hand, or perhaps both these factors combined. The same elements enter into all varieties of form or shape of which we are capable of forming an idea. Our ideas of distance, weight, resistance, all involve not merely sensory factors, but these combined with muscular movements. To revive any of these ideas is to revive both the sensory and motor elements of their composition, and we tend in ideation to repeat the actual movements which were concerned in the primary act of cognition. Ideas, therefore, except in so far as they are simple revivals of definite and uncomplicated sensory impressions, have no circumscribed habitation in the brain, but are the re-excitation of each and every one of the sensory and motor centres which are specially concerned in their acquisition. We know an orange by certain discriminated impressions made on the organs of sight, smell, taste, touch, and by certain muscular movements and sensations which give the form; and the re-presentation or idea of an orange is the associated re-excitation of the permanent cell-modifications, in each of the special sensory and motor centres primarily engaged in the act of cognition.

There is practically no limit to the number of associated combinations of sensory and motor elements. Sensory centres form organic associations with other sensory centres; motor centres with motor centres; sensory centres, simple and in complex association, with simple or complex associations of

motor centres. In this variety and complexity of permanent modifications, and organic cohesions between the sensory and motor centres of the hemispheres, we have the basis of all intellectual and volitional acquisitions. Each motor centre may enter into organic association with each and every sensory centre, each definite association being the representative of some consciously discriminated act. In the variety of associations between movements and sensations, some are loosely, some more firmly coherent; while one sensori-motor association is so constant as to give rise to the notion that the connection is indissoluble. This is the association between muscular movement and muscular sense, one in normal conditions so constant as to lead Bain to suppose that the latter is the inseparable concomitant of the motor impulse. I have endeavoured to show that the connection, though constant, is not inseparable; a distinction by no means a matter of hypercritical refinement, but a fundamental one, and one carrying with it the most important physiological as well as psychological issues.

The sensations accompanying muscular action being repeated as often as the muscular action itself, the organic nexus between the motor and tactile centres becomes so welded that this sensori-motor cohesion enters, like a compound chemical radical, as a simple factor, into every association which motor centres can form with other motor centres, and with sensory centres in general. Hence, in all volitional movements, the tactile sensory centres invariably functionate along with the motor centres, and give the extent and degree of the movement actually or ideally carried out. Bain would make the sensory a *proprium* of the motor, whereas it is only a contingent; in normal or physiological conditions an inseparable accident, but separable anatomically and pathologically.

§ 9. In respect to the development of the volitional control of the movements the conclusion has been reached that this is established when an organic cohesion has been welded between a consciously discriminated sensation or feeling and a definite and differentiated motor act. The volitional control of the individual movements having once been established, the work of education advances, and the conditions of

volitional action become more and more complex. The volition of the untutored and inexperienced infant is of a more or less impulsive character, and is conditioned mainly by impressions or feelings of the moment. Associations have not yet been found between the painful and pleasurable remote consequences of actions. *Experientia docet.* A child which has acquired the differentiated control of its limbs is impelled to touch and handle whatever strongly attracts its sight. The sight of a bright flame, like that of any other bright object, stimulates a desire to touch and handle it. This is followed by severe pain, and an association is formed between touching a certain brilliant object and severe suffering. The vivid memory of pain experienced on a former occasion is sufficient to counteract the impulse to touch when the child is again placed in similar circumstances. Here we have a simple case of the conflict of motives, and the inhibition or neutralisation of one motive by another and stronger. Action, if it results at all, is conditioned by the stronger. Similarly a hungry dog is impelled by the sight of food to seize and eat. Should the present gratification bring with it as a consequence the severe pain of a whipping, when certain articles of food have been seized, an association is formed between eating certain food and severe bodily pain; so that on a future occasion the memory of pain arises simultaneously with the desire to gratify hunger, and, in proportion to the vividness of the memory of pain, the impulse of appetite is neutralised and counteracted. The dog is said to have learnt to curb its appetite.

As experience increases, the associations between acts and consequences increase in complexity. Both by personal experience, as well as by the observed experience and testimony of others, associations are established between actions and their remote consequences as pleasures or pains, and it is found that present gratification may bring a future and greater pain, and actions causing present pain may bring a greater pleasure. As the great law of life is *vivere convenienter naturæ*—to secure pleasure and avoid pain in the highest and most general sense, and not for the moment only (a law which cannot be transgressed with impunity)—actions are conditioned no longer, as in the infant or untutored animal, by present desires

or feelings alone, but by present desires modified by the ideally revived feelings of pleasure or pain near and remote, which experience has associated with definite actions. The motive to action is thus the resultant of a complex system of forces; the more complex, the wider the experience, and the more numerous the associations formed between actions and their consequences, near and remote. Actions so conditioned are regarded as mature or deliberate, in contradistinction to impulsive volitions, but the difference is not in kind but only in degree of complexity; for in the end, actions conditioned by the resultant of a complex system of associations, are of essentially the same character as those conditioned by the simple stimulus of a present feeling or desire, where no other associations have as yet been formed capable of modifying it.

But what is normal in the infant or untutored animal may be positive insanity on the part of the educated adult. If in him actions are conditioned merely by present feelings or desires, irrespective of, or in spite of, the associations formed by experience between such acts and their consequences as pains, there is a reversion to the infantile type of volition; the only difference being that in the one case no opposing associations have as yet been formed, while in the other, though formed, they prove of no avail. An individual who so acts, acts irrationally; and if in anyone, notwithstanding the opposing influence of past associations, a present feeling or desire reaches such a pitch of intensity as to overbalance these associations, the individual is said to act in spite of himself, or, metaphorically, against his will. Such tendencies occur more or less in all, but they are exemplified more especially in certain forms of insanity, in which the individual becomes the victim of some morbid desire, and is impelled irresistibly, and to his horror, to commit some act fraught with dreadful consequences.

In the process of volitional acquisition the cohesions are chiefly formed between sensations and right-sided movements, so that the organic nexuses are established principally between the sensory centres and the motor centres of the left hemisphere, by which the movements of the right side are effected and governed.

§ 10. The growth of volition, the formation of permanent motor acquisitions, and the establishment of organic cohesions between the sensory and motor centres of the cerebral hemispheres are well illustrated in the acquisition of articulate speech. Commencing with spontaneous vocalisation and spontaneous movements of the articulatory apparatus, and encouraged and aided by imitative repetitions on the part of its teacher, the infant gradually acquires the power of associating a certain sound with a certain articulation, so that on the given sound the appropriate movements of the articulating and vocalising apparatus are called into play to reproduce it. An organic nexus becomes firmly established between the auditory and the articulating centres, and such nexuses become multiplied indefinitely, each articulate sound being represented by a definite sensori-motor cohesion—sound-articulation.

A further development of sensori-motor acquisition is the gradual establishment of links of association between certain visible characters and certain articulations, and this in such a manner that a certain visible symbol is recognised as the equivalent of a certain auditory impression, so that either can call up the proper articulation with definiteness and precision.

Here the articulatory or motor element is the central point of two sensory cohesions—the one auditory, the other visual—which two are regarded as equivalent.

In the case of the blind a similar cohesion may be formed between certain tactile impressions and the centres of articulation, so that at a definite tactual impression, as well as at a definite auditory impression, a definite articulate combination is called forth; and in the case of the deaf articulate speech is capable of being taught by means of the aid of vision directed to the movements of articulation. The articulate speech of the deaf fails only in respect of intonation and modulation, owing to the want of the guiding influence of the sense of hearing.

A still further stride in complexity is the acquisition of the power to represent, by movements of the fingers, symbols which, when seen, call up by association certain sounds and articulations.

Organic nexuses thus become established between the centres of hearing and articulation, between those of sight and articulation, or between those of touch and articulation; and complex nexuses between the centres of sight and sound, and the motor centres of articulation and manual movements.

These organic nexuses correspond to the acquisitions of spoken and written language, and the art of writing.

It is conceivable that all these simple and complex acquisitions and cohesions might be formed without any association having been established between certain articulate sounds or written symbols and certain objects or ideas; or, in other words, both spoken and written language might be acquired altogether apart from things signified. For the connection between words and things signified is nothing more than an association, words in themselves being only symbols. The association of articulate sounds with things signified is, however, generally preceded by, and proceeds *pari passu* with, the growth of the faculty of speech; so that the cohesion between the centres of hearing and articulation is rendered complex by the association of definite articulate sounds with certain objects seen, heard, touched, smelt, or tasted, or with objects of cognition in general.

Hence the articulation may be called into play not merely by a certain sound, but by the actual presentation or re-presentation of the object signified. The centres of articulation become, therefore, the central motor point of an immense number of sensory cohesions, all of which tend to evoke the articulation, and which, in turn, tend to be revived in idea by the actual or ideal articulation itself. The articulation is the essential fact, vocalisation being subordinate, and capable of being dispensed with altogether, as in whisper speech.

The primary associations in the acquisition of articulate speech being between sounds and articulations, as in spoken language, or between visible signs and articulations, as in written language, and between both these and things signified —directly in the former, and indirectly in the latter— secondary associations may be formed between visible signs and things signified, the link through articulation becoming subordinate, if not entirely dispensed with. A sound readily

calls up the thing signified, without the intervention of an articulation. It is, however, less common for a visible symbol to call up the thing signified without the intervention of articulation more or less suppressed. In the great majority of people there is observable a tendency during reading to translate the written symbols into their equivalent articulations. The less educated the person, and the less accustomed to reading, the greater is the tendency exhibited; and some persons cannot read intelligently without actually going through all the process of articulation represented by the written or printed characters.

§ 11. If the motor centres of the cerebral hemispheres are not merely the centres of impulse, but also the centres of registration and reproduction of volitional movements, it must follow that destruction of the motor centres will cause not merely paralysis of volitional movement, but also abolish all previous motor acquisitions.

If an individual should by education acquire the faculty of expressing his thoughts by symbolic dextral movements, the destruction of the manual motor centres of the left hemisphere will cause not only paralysis of the right hand, but also annihilate in ideation the association between thoughts and dextral movements. Such an individual, like the blind deaf-mute Laura Bridgman, would be rendered not merely hemiplegic, but aphasic by destruction of the manual motor centres of the left hemisphere. For the registration and revival of volitional movements must take place in the same centres as are primarily engaged and educated. Hence the memory and revivability of volitional movements must, as far as relates to the hand and arm, be principally in the left hemisphere, seeing that voluntary motor action and motor acquisition are in the great majority of people effected on the right side.

The motor centres of articulation present certain peculiarities both in their physiological and psychological aspects. Physiologically, as I have experimentally shown, each centre has a bilateral action. Hence destruction of the centre of articulation in the one hemisphere does cause paralysis of the articulatory apparatus, but only, if anything, a slight weakness or paresis of the opposite side. But while as regards the

mere physiological excitation of the muscles of articulation there seems to be little or no difference between the centres of articulation in the right and left hemisphere respectively, there is a marked difference, as shown by the facts of aphasia, between the two as regards the initiation and registration of the acts of articulation.

§ 12. In the disorders of speech resulting from cerebral disease classed under the terms *aphasia* and *amnesia* many of the principles above laid down in respect to the functions of the sensory and motor centres are strikingly exemplified.

The subject of aphasia [1] is deprived of the faculty of articulate speech, and also very generally of the faculty of expressing his thoughts in writing, while he continues intelligently to comprehend the meaning of words spoken to him, or, it may be, to appreciate the meaning of written language. An aphasic individual knows perfectly well—as exhibited by his gestures—if a thing is called by its right name or not, but he cannot utter the word himself or write it when it is suggested to him. In his attempts, only an automatic or interjectional expression or some unintelligible jargon escapes his lips, or unmeaning scrawls are set down on paper as writing.

This affection is usually, at first at least, associated with a greater or less degree of right hemiplegia, but the motor affection of the right side, chiefly of the right arm, is often slight and transient, or may be wanting from the first, the only indication of motor paralysis being a paretic or weak condition of the oral muscles of the right side.

The inability to speak is not due to paralysis of the muscles of articulation, for these are set in action and employed for purposes of mastication and deglutition by the aphasic individual. It is only when the centres of articulation are destroyed on both sides that complete paralysis of the articulatory apparatus occurs as well as aphasia.[2]

The cause of this affection was shown by Broca—and his observations have been confirmed by thousands of other cases—to be associated with disease in the region of the posterior

[1] By the term in this signification is meant aphasia proper—Broca's or motor aphasia.

[2] See case reported by Barlow, *Brit. Med. Journ.*, 1877.

extremity of the third left frontal convolution, where it abuts on the fissure of Sylvius, and overlaps the island of Reil; a region which I have shown corresponds with the situation of the motor centres of articulation in the monkey (see fig. 70, (9) and (10)).[1]

[1] I do not consider it necessary, in the present state of clinical medicine and pathology, to enter at length into cases and arguments in favour of the definite localisation of the lesion causing aphasia. I take it as established beyond all possibility of doubt that lesions in the region indicated above do in the overwhelming majority of instances cause aphasia, and the problem before us is to explain why such lesions should cause aphasia and leave other faculties intact. It is utterly beside the point to argue that loss of speech is not in all cases due to localised disease of this nature, for naturally whatever causes paralysis of the muscles of articulation will cause inability to speak; and whatever interrupts the processes of ideation and thought, such as sudden shocks of emotion or the like, will also cause inability to speak. Such states cannot properly be classed under the head of aphasia, where we have a definite condition of loss of speech, while all other faculties—sensation, emotion, thought, and volition—remain practically unimpaired.

In reference to the arguments of the opponents of localisation, if such still exist, I would quote with the fullest concurrence the following passage from Dr. Broadbent, written in 1872, which the observations of the intervening years only serve to corroborate and confirm: 'The question being one of primary interest in cerebral physiology, I have examined all the apparently exceptional cases of which I have been able to find the published record; and it is remarkable how large a proportion of them break down under careful scrutiny. Setting aside the distinction between the conditions to which the terms amnesia and aphasia have been applied, I have found, described under the head of aphasia, cases of labio-glosso-pharyngeal paralysis on the one hand, and of dementia on the other; and, again, the speechlessness or indistinct articulation of patients who have never fully recovered from the shock of an apoplectic or convulsive attack, or of embolism of a large cerebral artery. Cases are quoted as examples of aphasia without disease of the left third frontal convolution in which the left middle cerebral artery, the nutrient vessel of the part, was blocked up; in which, therefore, the persistence of speech would have constituted a graver objection to the views in question than its loss; or in which, without apparent disease of the surface grey matter, the convolution was cut off from the central ganglia and the rest of the cerebrum by lesion of its white fibres; in some instances again aphasia has been fugitive, and therefore dependent on some temporary condition; and yet the cases have been considered exceptional because no permanent lesion has been found after death. On the other hand, cases have been described as examples of disease of the left third frontal gyrus without affection of speech, in which the description of the lesion clearly shows that the observer has taken some other convolution for the one named' ('Mechanism of Thought and Speech,' *Medico-Chirurgical Transactions*, vol. lv. 1872). See also Kussmaul's monograph, 'Die Störungen der Sprache,' Ziemssen's *Cyclopædia*, 1877.

One of the most common causes of the affection is softening of this region, consequent on sudden stoppage of the circulation by embolic plugging of the arterial channels which convey its blood-supply, by which the functional activity of the part is temporarily or permanently suspended.

Owing to the proximity and common vascular supply of the motor centres of the hand and facial muscles, it is easy to see how they also become implicated in the lesion of the centres of articulation, and why, therefore, dextral and facial motor paralysis should so commonly occur along with aphasia. This may be taken as evidence in proof of the fact that lesions of the cortical motor centres cause motor paralysis on the opposite side.

The escape of the articulatory muscles from paralysis in unilateral lesion of the centres of articulation is accounted for by the bilateral influence of each centre which has been experimentally demonstrated.

The loss of speech from destruction of the centres of articulation is not more difficult of explanation on the principles laid down in this chapter than the loss of sight presentatively or re-presentatively from destruction of the visual centre. That which constitutes the apparent difficulty is the explanation of speechlessness without motor paralysis from lesion of the centres of articulation in the left hemisphere.

This difficulty is explicable on the principles laid down in reference to motor acquisitions in general. As the right side of the body is more especially concerned in volitional motor acts, so the education is principally in the motor centres of the left hemisphere, and these centres are more especially the organic basis of motor acquisitions. The left articulatory centres, as has been argued by more than one observer, preponderate over the right in the initiation of motor acts of articulation. They are, therefore, more especially the organic basis of the memory of articulations and of their revival. The destruction of the left articulatory centres removes the motor limb of the cohesions which have been formed by long education between the centres of hearing and sight, and between the centres of ideation in general.

Sounds actual or revived fail to excite the appropriate

articulations. The individual is speechless, the motor part of the sensori-motor cohesion, sound-articulation, being broken. The sight of written symbols also fails to reproduce the equivalent articulatory action. The individual is speechless because the motor element of the sensori-motor cohesion, sight-articulation, is broken.

Ideally revived sights, sounds, touches, tastes, smells, fail to call up the symbolic articulations; hence the individual cannot express his ideas in language: and in so far as language or internal speech is necessary to complex trains of thought, in that proportion is thought impaired. Thought, however, may be carried on without language, but it is thought in particulars, and is as cumbrous and limited as mathematical calculations without algebraical symbols. Thought, as has been observed by Bain, is in a great measure carried on by internal speech, i.e. through the ideal or faint re-excitation of the articulatory processes which are symbolic of ideas. This is shown by the unconsciously executed movements of the lips and tongue which all persons exhibit more or less, and some so obviously that the unconscious processes rise almost to the point of whispering. So also the blind deaf-mute Laura Bridgman, whose language was symbolic movements of the fingers, during thought or when dreaming, unconsciously executed the same movements as she was accustomed to make in the actual exercise of her manual speech.

And just as ideas tend to excite their symbolic representations in articulation or in manual movements, so does the revival of the articulatory or manual movements tend by association to call up the other limbs of the cohesions, whether simple sights, sounds, tastes, smells, or their combinations. The importance of this connection between the articulating centres and the centres of ideation in general will be shown more fully in reference to the voluntary revival of ideas and control of ideation.

§ 13. We have seen that a person aphasic from destruction of his speech centre (as we may for shortness call the articulatory motor centres of the left hemisphere) still remains capable of appreciating the meaning of words uttered in his hearing. In this respect he does not (and there is no reason

why he should) differ from a normal individual. His centres of sight, hearing, &c. being unimpaired, he is as capable as before of visual, auditory, tactile, gustatory, and olfactory ideation. The difference consists in the fact that in the aphasic individual the word spoken, though it calls up the idea or meaning, cannot evoke the word itself, owing to the centres of word-execution and word-registration being destroyed. The appreciation of the meaning of spoken words is readily accounted for by the fact that in the process of education an association is formed directly between certain sounds and certain objects of sense, simultaneously with, if not antecedent to, the formation of the cohesive association between these sounds and certain acts of articulation. The cohesion or association between sound and meaning remains unimpaired in aphasia: it is the cohesion between sound and articulation which is broken by removal of the motor factor of the organic nexus.

The association between written symbols and things signified is, however, secondary to the associations formed between sounds and things signified, and between sounds and articulations, for speech precedes the art of writing. In the first instance, when an individual is learning to read, written symbols are translated into articulations and revived sounds before they call up the things signified. This translation occurs in all at first, and continues apparent in those persons not much accustomed to reading, for they only understand by articulating in a more or less suppressed manner all the while. Just as an individual in learning a foreign language is at first obliged to translate the words into his vernacular before he reaches the meaning, but comes by familiarity and practice to associate the new words with their meaning directly without the aid of the vernacular, and even to think in the new language, so it is possible that, by long experience in reading, a direct association may be established between written symbols and things signified, without the mediation of articulation. In such a case a person who has his speech centre disorganised will still be able to comprehend the meaning of written language. A person, on the other hand, who has not established the direct association between written symbols and

things signified, and is still obliged to translate through articulation, will, by destruction of his speech centre, fail to comprehend written language, though he may still understand spoken language.

In learning to write a new association has to be grafted on to the association already formed between sounds and articulations. The new cohesion is between sounds and certain symbolic manual movements guided by sight, which symbolic tracings are the equivalents of certain acts of articulation. In the first instance this association between sounds, or sounds and things signified, and manual movements, takes place through the mediation of the centres of articulation; for the sounds or ideas are first reproduced actually or internally by articulations before their equivalence in written symbols is established and recognised.

By education, and practice in expressing ideas in written symbols, a direct association becomes established between ideas and symbolic manual movements, without the intervention of articulation; and in proportion as the translation through articulation is dispensed with, in that proportion will an individual continue able to write who is aphasic from disease of his speech centre. In the great majority of cases of aphasia met with in hospitals the direct association between ideas, or articulate sounds, and manual equivalents of articulations has not been established, except for very simple and constantly repeated acts of writing, such as signing one's name; and hence, as the intervention of articulation is still necessary before ideas can be expressed in writing, destruction of the speech centre causes not merely aphasia, but also agraphia, or loss of written language. To these considerations must be added the fact that in a large proportion of the cases of aphasia the manual motor centres are also more or less damaged, so that agraphia may be in part due to the direct impairment of the associations formed between ideas and certain highly specialised manual movements.

Examples of all these different conditions are to be met with among aphasics. Some can neither speak nor write; some can write, but cannot speak; some can write their names, but cannot write anything else; all can comprehend spoken

language ; many can comprehend written language ; others not at all, or very imperfectly. Between the normal condition of the speech centre and its total destruction many intermediate abnormal conditions occur, which show themselves in partial disorders of speech, inco-ordinate or defective. It is a common observation that persons lose from their vocabulary proper names and substantives more readily than words expressing the relations and qualities of objects and ideas. This leads to more or less cumbrous periphrases in order to express what would otherwise be summed up concisely in a single word.

These and other similar defects are readily explicable, as Kussmaul has correctly indicated,[1] on the principle that the more loose the cohesion between objects or ideas and names, the more readily do such words fall out of the vocabulary by any conditions which tend to the impairment or dissolution of the centres of word execution and registration. The more concrete the object, the less do we require a symbol wherewith to remember and think it. We can think of individuals and objects apart from their names, so that, as the association of such objects of ideation with words is but slight, it is the first to give way. The abstract qualities and relations of objects, however, exist only by reason of words, and therefore the association of such ideas with words is a fundamental one, and the last to give way before any dissolving lesion of the word centres. Hence the terms expressing qualities and relations are retained more vividly and persistently than those expressing mere particulars or concretes. Similarly the initial letter of a word is more persistent in memory than the rest of the word, and we can often remember how the word begins, and of how many syllables it is composed, without being able to recall the word itself. So we are able frequently to remember where a passage occurs in a book when we have entirely forgotten and are unable to recall the passage itself or the statements it contains.

§ 14. The speech centre is, as has been stated, in the great majority of instances situated in the left hemisphere. But there is no reason, beyond education and heredity,[2] why this

[1] 'Die Störungen der Sprache,' p. 164, Ziemssen's *Cyclopædia*, 1877.

[2] Why dextral pre-eminence should occur in the first instance is not quite

should necessarily be so. It is quite conceivable that the articulating centres of the right hemisphere should be educated in a similar manner. A person who has lost the use of his right hand may by education and practice acquire with his left all the cunning of his right. In such a case the manual motor centres of the right hemisphere become the centres of motor acquisitions similar to those of the left. As regards the articulating centres, the rule seems to be that they are educated, and become the organic seat of volitional acquisitions on the same side as the manual centres. Hence, as most people are right-handed, the education of the centres of volitional movements takes place in the left hemisphere. This is borne out in a striking manner by the occurrence of cases of aphasia with left hemiplegia in left-handed people. Several cases of this kind have now been put on record.[1]

These cases more than counterbalance any exception to the rule that the articulating centres are educated on the same side as the manual motor centres. The rule need not be regarded as absolute, and we may admit exceptions without invalidating a single conclusion respecting the pathology of aphasia as above laid down. An interesting case has been reported by Wadham[2] of aphasia with left hemiplegia occurring in a young man belonging to a family of *gauchers*. Yet this person had learnt to write with his right hand, so that as regards speech he was right-brained, but as regards writing he was left-brained.

Though the left articulatory centre is the one commonly and specially educated in speech, it is quite conceivable that a person who has become aphasic by reason of total and permanent destruction of the left speech centre may re-acquire the faculty of speech by education of the right articulatory centres. To a certain extent they have undergone education along with those of the left through associated action, regis-

satisfactorily made out. See on this W. Ogle, 'On Dextral Pre-eminence,' *Med.-Chir. Trans.*, 1871, p. 279.

[1] *Vide* Mongié, *De l'Aphasie*, Thèse, 1866; Russell, *Medical Times and Gazette*, 1874; and other cases by Pye-Smith, Hughlings-Jackson, W. Ogle, quoted by Kussmaul, *op. cit.* p. 147. Notes of a similar case were also communicated to me by Dr. Lauder Brunton.

[2] *St. George's Hosp. Reports*, vol. iv.

tering automatically, as Hughlings Jackson puts it, the volitional acts of the left. This automatic may be educated into volitional power, though at the age at which aphasia usually occurs, there is less capacity and plasticity in the nerve centres for forming new cohesions and associations. The rapid recovery which so frequently occurs in cases of aphasia, especially of the kind due to embolic plugging of the nutrient arteries of the left centres, is not to be regarded as an indication of the education of the right centres, but rather of the re-establishment of the circulation and nutrition in parts only temporarily rendered functionless.

But there are other cases which would seem to show that recovery of speech may take place after a lesion which has caused complete and permanent destruction of the left speech centre. A case which seems to me to be of this nature has been reported by Drs. Batty Tuke and Fraser ('Journal of Mental Science,' April 1872), who, however, have adduced it as an instance opposed to the localisation of a speech centre, which in one sense—i.e. as against absolute unilateral localisation—it certainly is. The case in essentials is that of a female patient who was rendered unconscious by the occurrence of cerebral hæmorrhage. On her recovery she was found totally speechless, and she remained so for an indefinite period. In process of time, however, the faculty of speech was restored in great measure, though never quite perfectly. 'During the whole period of her residence two peculiarities in her speech were observed—a thickness of articulation resembling that of general paralysis, and a hesitancy when about to name anything, the latter increasing very much some months previous to her death.

'The thickness seemed apparently due to slight immobility of the upper lip when speaking, but there was no paralysis when the lip was voluntarily compressed against its fellow. The inaction of the upper lip was observed by all.

'The hesitancy was most marked when she came to a noun, the hiatus varying in duration according to the uncommonness of the word. Latterly she could not recall even the commonest terms, and periphrases or gestures were used to indicate her meaning. She was always relieved and pleased

if the words were given her, when she invariably repeated them. For example, she would say, "Give me a glass of——" If asked if it was "water?" she said, "No." "Wine?" "No.' "Whisky?" "Yes, whisky." *Never did she hesitate to articulate the word when she heard it.*'

Death occurred fifteen years after the seizure, and it was found *post mortem* that there was total destruction and loss of substance in the cortical region in the left hemisphere corresponding with the position of the centres of articulation. This seems to me one of the clearest cases of reacquisition of the faculty of speech by education of the articulating centres of the right side. That speech was lost in the first instance is in harmony with the usual effect of lesion of the left speech centre. Education of the right side had not become quite perfect even after fifteen years, and that peculiar hesitancy, and the fact, which the authors themselves have specially noted in italics, that speech often required the aid of suggestion, is in accordance with the less volitional and greater automatic power of the right hemisphere.

§ 15. Intimately related with, and very frequently complicating, motor aphasia, as above defined, are a series of disorders of speech dependent on lesions of the sensory centres and tracts by and through which impressions are perceived and associated with definite acts of articulation. These disorders are classed under the head of amnesia or sensory aphasia. We have seen that a person speechless by reason of destruction of his articulatory centre alone is still capable of comprehending the meaning of spoken language, and also, to a greater or less extent, of written language, though he cannot name anything, or make any utterance beyond an automatic or interjectional expression altogether irrelevant. With this is usually associated some degree of agraphia, though aphasia and agraphia do not necessarily run parallel to each other.

In the class of disorders of language now under consideration, of which two chief groups or divisions are recognised, the individuals can both speak and write, often with remarkable fluency. In the one group the individuals cannot comprehend spoken language, or repeat what is said in

their hearing, while they can readily articulate written language; in the other group they are unable to interpret written language, or even what they themselves have written, while they readily understand what is said to them, or can write from dictation. Occasionally the two conditions are more or less intermingled, or complicated with aphasia proper.

The inability to understand written language has been termed by Kussmaul[1] 'word-blindness' (*cæcitas verbalis*), and the inability to understand spoken language, 'word-deafness' (*surditas verbalis*).

Word-blindness, which in its different degrees is an impairment or complete interruption of the association formed between written symbols and their equivalent articulations, and with things signified, has been found, in the comparatively few cases as yet investigated *post mortem*, to be associated with lesion more particularly of the angular gyrus of the left hemisphere.[2] This, as we have seen, is a fundamental portion of the visual centre.

The condition is not dependent on defective vision (though sometimes complicated with hemiopia), for the individuals affected can see minute objects and can copy writing or designs; nor is it dependent on defective visual ideation in general, for objects and their uses are recognised, though occasionally visual ideation is impaired. Thus mistakes are sometimes made as to the value of coins, and objects are used for purposes for which they are unfitted; as, for instance, a fork instead of a spoon to eat soup.

The essential, and frequently the only, defect is the inability to read, or interpret the meaning of written or printed characters.

From the fugacious character of partial and unilateral lesions of the visual centres, as above exemplified, it is easy to account for the absence of any evident impairment of visual perception in the 'word-blind'; and the bilateral relations of the eyes, and the associated action of the hemispheres, will

[1] *Op. cit.* See also an excellent memoir, *De la Cécité et la Surdité des Mots dans l'Aphasie*, by Nadine Skwortzoff. Paris, 1881.

[2] See Broadbent's case, *Med.-Chir. Trans.* 1872. Déjérine's case, reported by Skwortzoff, *op. cit.*

suffice to account for the retention of visual ideation in general, even though considerable damage should be inflicted on the visual centre of one hemisphere.

The facts relating to word-blindness show that the association of written symbols with things signified is a function more particularly of the visual centre of the left hemisphere, the same in which the centre of articulation is developed for purposes of speech. The association of written symbols with things signified is, as has been before remarked, secondary to the association between things signified and acts of articulation, for speech precedes the act of writing. Written symbols are merely, as Hughlings Jackson[1] aptly terms them, 'symbols of symbols of images.' The association between visible symbols and things signified is therefore an indirect and comparatively loose one. Being so, it is an association which gives way sooner before a destructive or dissolving[2] lesion of the centres of vision than the more fundamental functions of visual perception and concrete visual ideation.

There are degrees of word-blindness, just as there are degrees of aphasia proper. Certain written symbols, like certain words, persist longer than others, or are less readily lost. An individual word-blind to all other words may still recognise his name at sight. His own name is more fundamentally organised in his visual centres than any other visual symbol. A word-blind may also recognise and pronounce the individual letters of words, while the words themselves are absolutely unintelligible and unpronounceable. Usually the word-blind can neither recognise the meaning of the words directly nor can he make the equivalent articulations, and so reach the meaning indirectly. In one remarkable case on record,[3] however, a patient gifted with unusually vivid powers of visual memory and ideation, suddenly, from some undetermined condition, lost his powers in this respect, so that all

[1] 'On Affections of Speech from Disease of the Brain,' *Brain*, vols. i. and ii. 1878–1880.

[2] See Hughlings-Jackson's brilliant and suggestive Croonian Lectures on 'Evolution and Dissolution of the Nervous System,' *Brit. Med. Journ.* 1884.

[3] Under the care of Charcot, reported by Bernard, *Progrès Médical*, 1883, p. 568.

things, even his own person, seemed strange and unfamiliar to him. Though visual symbols were of themselves unintelligible, he was able to articulate them, and was thus able to comprehend their meaning indirectly through articulation and the revived sounds.

A word-blind can speak and express his ideas in writing, or write from dictation; but, though it may seem almost incredible, he cannot read or understand a syllable of what he has just written. But, like the blind man, he may learn to read what he has written, and written characters in general, by the aid of his sense of touch and the sensations accompanying muscular movements. Several examples of this are on record. Westphal [1] relates the case of a word-blind re-acquiring the art of reading by passing his fingers over the letters, just as if he were rewriting them, and spelling them out as he went on. In a similar case Magnan [2] taught the patient to recognise and read raised letters by the sense of touch. Considerable progress was made, but at best only one letter—the letter O—was recognised directly by sight alone. In another case, related by Charcot,[3] the individual arrived at the meaning of words which he was unable to read by making symbolic writing movements while fixing his eyes on the page. He could read written characters more readily than printed ones, as he was naturally more familiar with the sensations which would be associated with the act of writing than of drawing printed letters.

It is evident, therefore, that in word-blindness we have a defect in visual ideation only, while ideation otherwise is unaffected; and this defect is clearly proved to be in relation with lesion of the visual centre and its connections with the centres of articulation.

We have reason to believe, from the facts of experiment as well as those of clinical observation,[4] that complete destruction

[1] Quoted by Kussmaul, *op. cit.* p. 180, from *Zeitsch. f. Ethnologie*, 1874.

[2] Skwortzoff, *op. cit.* obs. vii. p. 44.

[3] 'Des differentes Formes de l'Aphasie,' *Progrès Médical*, 1883, p. 441.

[4] A case is reported by Shaw (*Archives of Medicine*, Feb. 1882) in which the angular gyrus and superior temporo-sphenoidal convolution (centres of vision and hearing) were destroyed symmetrically in both hemispheres. The

of the visual centre in both hemispheres would abolish visual perception and visual ideation altogether. This condition would profoundly diminish the scope of human intelligence; but even in such case, if congenital, and with deaf-mutism superadded, as illustrated by Laura Bridgman, a considerable degree of intelligence might be manifested through the agency of the remaining sensory centres.

§ 16. 'Word-deafness,' which in its different degrees is a defect or complete interruption in the association of articulate sounds with acts of articulation and things signified, has been found to depend on lesions involving the superior temporo-sphenoidal convolution[1] (specially of the left hemisphere) which, as we have seen from the experiments above recorded (Chapter IX. § 15) is the auditory centre. The word-deaf is not deaf to sounds, for he can hear the ticking of a watch; nor to music, for he can recognise and hum an air; but articulate sounds, except, perhaps, his own name, or the simplest command which he is accustomed to act on automatically,[2] have no meaning, and cannot be repeated. Yet the individual so affected can speak and, it may be, read and write. The speech of the word-deaf is, however, though not always, often of a very extraordinary and unintelligible character. Though he may speak fluently, and with lively gesture and intonation, his utterances are frequently mere jargon—words mixed up without regard to grammar or sense—and convey to others none of the meaning which he evidently attaches to them.

In all persons except deaf-mutes the centres of articulation

patient was both blind and deaf, and at the same time utterly demented and incoherent.

[1] Wernicke's case, *Der aphatische Symptomencomplex*, 1874; Broadbent's case, a case of amnesia, *Med.-Chir. Trans.* vol. lxi. 1878; D'Heilly and Chantemesse's case, *Progrès Médical*, No. 2, 1883; Seppili (*Revist. Speriment. di Freniat*, vol. x. 1884) finds that of seventeen cases in all, in which a post-mortem examination was made, *in every one* there was lesion of the superior temporo-sphenoidal convolution, and twelve in which also the second or middle convolution was involved.

[2] This I observed in a case under my own care. The patient, without any leading gestures, understood and acted on the simple commands, 'Stand up!' 'Sit down!' and the like, but all complex sentences were apparently utterly unintelligible.

are set in action in response to, and are guided mainly by, articulate sounds. Deaf-mutes articulate and phonate guided by the sense of vision and the sensations which accompany the acts of articulation and phonation.

Though, therefore, it is possible that the processes of articulation in connection with ideation may be set in action, and be guided correctly by the sensations accompanying the movements of articulation, altogether apart from the sense of hearing, yet as in all persons not deaf-mutes acts of articulation are primarily made in response to, and with a view to reproduce, certain symbolic sounds, it is natural to expect that defect in the registration and ideal revival of the sounds associated with acts of articulation should lead to disorders of utterance. Of these the individual, owing to his defective auditory register, is either not aware at all, or he may have some dim consciousness that he has not used the proper word to express his meaning. It is, however, theoretically possible that such patients might be taught to speak correctly in the same way as deaf-mutes are taught lip-speech, viz. by the aid of vision and the muscular sense.

Of those affected with word-deafness some are able to read intelligently, others apparently not at all or very imperfectly. The differences will be found to depend on whether direct associations have been established, or not, between visual symbols and things signified. In the former case the written or printed characters will call up the meaning directly without the mediation of the centres of articulation and sounds. If, however, articulation more or less suppressed and the associated actual or ideal revival of the equivalent symbolic sounds should be necessary, as it undoubtedly is in the large majority, in order to arrive at the thing signified by the written characters, it is obvious that in such cases word-deafness must lead to alexia, or inability to read, according to the degree in which the translation of written symbols into their equivalent sounds is necessary. My own patient, unable to understand spoken language, read and answered simple questions put to him on a slate which he carried for the purpose. But I satisfied myself that he only very imperfectly comprehended the sense of a paragraph in the newspaper which I placed

before him. He read and re-read, and after some time, during which he made the remark, 'It loses my head,' he gave me a very imperfect account of the subject matter.

It would seem at first sight very unlikely that a word-deaf individual, whose words are a disconnected jumble, should be able nevertheless to write correctly. Yet that such is possible is shown by Magnan's[1] case, nor is this difficult to explain. Whereas, owing to the defect of auditory registration, the word spoken vanishes, and if wrong cannot be rectified, *litera scripta manet* and serves, through the visual sense, as a guide to the appropriate combination and composition.

In those cases of word-deafness in which all connected writing, beyond mere letters or scrawls, seems impossible, we may assume that, just as in regard to reading, internal speech and the revival of the symbolic sounds are necessary before images or ideas can be expressed in written symbols. Hence as the ideal revival of the equivalent sounds is impossible or imperfect, so also must be the expression of ideation in writing.

Language is associated more particularly with the centres of visual and auditory perception and ideation. Next in importance to these comes the sense of touch, and we can name some things very readily by touch alone without the aid of sight or hearing. The blind man reads by touch. Certain tactile symbols are recognised as the equivalents of certain articulate sounds, and, in time, more or less directly as the equivalents of certain images or objects of ideation. Just as an individual becomes word-blind from lesion of his centres of visual ideation, so a blind man who has learnt to read by touch should become 'word-anæsthetic' by lesion of his centres of tactile perception and ideation (the falciform lobe). We should thus have an *anæsthesia* or *apselaphesia verbalis*, parallel with a *cæcitas* and *surditas verbalis*. It is conceivable in like manner that we might have an *anosmia verbalis* and an *ageusia verbalis*, an inability to associate things smelt or tasted with their symbolic articulations. Usually

[1] See Skwortzoff, *op. cit.* obs. vii. 'Ne sachant nommer aucun objet, *ne prononçant que des mots isolés ou des phrases décousues*, il pouvait cependant bien lire et écrire facilement sans faire une faute.'

things smelt and tasted are objects also of visual perception and ideation, but it is possible that, vision and other senses apart, the mere smell or taste should evoke the symbolic articulation as readily as any of the other sensory characters of the object. It is therefore extremely probable that lesion of the centres of olfactory and gustatory perception and ideation in the left hemisphere may produce verbal anosmia or ageusia. I am not aware that as yet any such cases have been observed. But if so, such facts would indicate lesion of the centres themselves, rather than of the tracts which convey to them impressions conditioned by odorous or sapid stimuli.

§ 17. It has been assumed by several writers, among others by Hughlings Jackson,[1] that in addition to the sensory and motor substrata, which have been demonstrated and defined by physiological and clinical research, there are other and higher motor as well as sensory centres in which all the motor and sensory functions are again represented, and form the substrata of the higher mental operations. This hypothesis receives no confirmation from the facts of experiment, nor does it appear to me at all necessary to explain the facts either of normal or abnormal 'mentation.' We have in the sensory and motor centres of the cortex the substrata of the respective forms of sensory perception and ideation, and of the individual acts of volition, simple and compound, as well as of the feelings associated with their activity. It seems more reasonable to suppose that there may be higher and lower degrees of complexity or evolution in the same centres than to assume the separate existence of more highly evolved centres, for which no evidence is obtained by the results of experimental research. In the sensory and motor centres, experimentally defined, we have the elements of the simple and compound cognitions and acts of volition. But while feelings, present or revived, tend to excite action in a purely reflex manner, and ideas excite ideas along the lines of association embraced generally under the heads of contiguity and similarity, there is implied in all the higher mental operations, such as abstraction, deliberation, constructive association, and the

[1] 'Evolution and Dissolution of the Nervous System,' *Brit. Med. Journ.* 1884.

like, a power of controlling the current of feeling and ideation, and of concentrating consciousness on one object, or one particular class of ideas or objects, to the exclusion of all others. The control of ideation and the power of attention form the basis of all those intellectual achievements not included in mere receptiveness, ideational or emotional mobility, and the facility of executing delicate and complex motor acts. These powers are in their nature truly voluntary, and depend essentially, as has been clearly recognised by Bain and Wundt, on volitional movements. We have, however, no direct control over the current of ideation, any more than we have the power of calling up a sensation at will. But as we may indirectly call up sensations by adapted voluntary movements, so indirectly we may react upon our ideational centres by making the movements with which certain ideas or feelings cohere. By imitating the physical expression of emotions we may succeed in inducing the corresponding mental states. We cannot feign a painful emotion without making the appropriate facial expression, and still less maintain it if we assume the opposite expression. We cannot feign grief with a smiling countenance. Though there are limits to our powers in this respect, and in some much narrower than in others, yet we can considerably modify the current of ideation and feeling by making volitional movements of an opposite character to those which the feelings we are endeavouring to combat naturally excite, or such movements as will bring us in relation with a new set of impressions, calculated to overwhelm or neutralise the feeling or idea which we seek to banish from our minds. The physical embodiment of emotions, and the special characteristics of each, are well known and universally recognised. Less apparent, but none the less real, are the muscular movements associated with ideation or thought removed as far as possible from mere feeling. Through these 'thought-reading' may be, and is, daily accomplished to a greater or less extent by every keen observer of human beings.

'It is not obvious at first sight that the retention of an *idea* in the mind is operated by voluntary muscles. Which movements are operating when I am cogitating a circle or recollecting St. Paul's? There can be no answer given to this

unless on the assumption that the mental, or revived, image occupies the same place in the brain and other parts of the system as the original sensation did. . . . Now, there being a muscular element in our sensations, especially of the higher senses—touch, hearing, and sight—this element must somehow or other have a place in the after remembrance or idea. The ideal circle is a restoring of those currents that would prompt the sweep of the eye round a real circle; the difference lies in the last stage, or in stopping short of the actual movement performed by the organ. We can direct the currents necessary for keeping an imagined circle in view by the same kind of impetus as is required to look at a diagram in Euclid.'[1]

In calling up an idea, therefore, we are in reality making in a more or less suppressed manner the movements with which the ideas are respectively associated in organic cohesion. And just as sensory impressions or ideas tend to call up movements, so the excitation of movements tends to call up by association the various sensory factors with which these particular movements cohere. The excitation of the motor centres, not sufficient to diffuse itself in actual movement, expends its force internally along the lines of organic cohesion, and the various factors which have become coherent with any particular movement rise into consciousness. As the tugging at a plant with branching roots sends a vibratile thrill to the remotest radicle, so the tension of the motor centre keeps in a state of conscious thrill the ideational centres organically coherent therewith.

The intervention of volitional movements in ideation is most apparent in the case of concrete ideation; such as when we think of a particular object possessing form and extension, our notions of which have been largely gained by the sensations accompanying ocular and manual movements. So also when we are recalling qualities of taste and smell, in the acquisition of which certain special movements are called into play. The muscular element in the recall of ideas of sound and colour, and of the abstract relations and qualities of objects in general, is at first sight obscure; but when we remember that thought is in a large measure internal speech, and that the abstract relations and

[1] Bain, *The Emotions and the Will*, 1875, p. 370.

qualities of objects are inseparably bound up with words, we can readily see that we may call up the images symbolised in words, however abstract they may be, by making the articulatory movements in which we have symbolised them. We recall the image or idea by pronouncing its name in a more or less suppressed manner; a fact which is plainly evident to all who pay attention to their own ideational processes.

§ 18. Ideas excited peripherically, arising spontaneously, or recalled voluntarily, tend to flow along the lines of association by contiguity or similarity. The current may flow on uninterruptedly as in a reverie or a dream, or it may be suddenly checked or diverted by an impression from without, which vividly engages our attention. Attention so excited is purely passive, and the concentration of consciousness is proportional to the intensity of the stimulus. But just as we can at will fix our gaze on some one object out of many appealing to our sense of vision, and see this clearly while all others are indistinct or invisible, so we can fix our intellectual gaze, or concentrate our consciousness, on some one idea or class of ideas to the exclusion of all others in the field of intellectual vision. This is a purely volitional act, and its exercise is accompanied by a distinct feeling of exertion, and ultimately fatigue if continued.

The physical expression of rapt attention is that of intent gaze, with the eyes accommodated for near or distant objects, and associated with such movements of the head as serve to bring the object on the punctum centrale of the retina. These facts indicate that intellectual attention is essentially ideal vision, and that when we are engaged in attentive ideation we are making precisely the same movements of the head and eyes as are necessary for clear actual vision. Though many individuals when engaged in deep thought close their eyelids in order to keep out distracting images, the eyes themselves maintain the position of actual gaze, near or distant, according to the nature and position of the ideal object. When we think of a large or distant object the eyes are divergent or parallel; when we think of a small or near object the optic axes converge.

Apart from the passive or reflex concentration of conscious-

ness conditioned by the intensity of the spontaneously revived or actual sensation, we cannot voluntarily concentrate attention on any idea which we cannot represent visually, either in its own characters, source, or relations. Thus sounds which have no direct visual characters can—actual reproduction apart—be thought of only indirectly by picturing the source, the instrument, or the circumstances under which we have actually heard them. When the ideal object is held in the field of clear vision by the appropriate ocular movements, the natural laws of association, combined with our power of controlling the current of ideation through articulatory and other movements, enable us to follow the idea in all its relations and ramifications.

If intellectual attention is mainly ideal vision it must follow that the faculty of attention, with all that it implies in the sphere of intellectual operations, must be intimately related to the volitional control of the head and eyes in association with the centres of visual perception and ideation. Just as the initiation, or partial excitation, of any particular movement reacts back upon the sensory cohesions with which it is associated, so the movements of the head and eyes react back on the centres of vision and keep the ideal object in the field of clear consciousness, and through this recall its various sensory and motor associations.

It is not essential that the object revived in idea should be so clearly revived in the visual field as the actual object itself. There are great differences in this respect among different individuals,[1] and there is no relation between the vividness of the mental imagery and the faculty of attention and abstract thought. It is, in fact, more conducive to abstract thought that the visual images should not have concrete sharpness, but rather the character of symbols or counters, which are more mobile and manageable than the images themselves with all their details filled in.

Expectant attention greatly reduces the time otherwise requisite for the completion of the mental processes intervening

[1] See the valuable and interesting observations on this head by Francis Galton, *Inquiries into Human Faculty and its Development*, 1883; *Mental Imagery*, pp. 83 *et seq.*

between the reception of an impression and the appropriate act of volition it should call forth. Picturing the situation, we are able to place the organs of sensation in the most favourable position for the reception of the impression, and we already half-perform—by throwing the muscles into a state of tension—the muscular act which is to signalise the completion of the mental process itself.

§ 19. The reactions consequent on electrical stimulation of the angular gyrus and superior temporo-sphenoidal convolution are evidently of the character of reflex movements, indicative of attention directed towards the supposed origin of the visual and auditory sensations aroused subjectively by the stimulus. That the reactions in question are in this case merely reflex or associated movements is shown by the fact that destruction of these regions, unilaterally or bilaterally, causes no impairment of the movements of the head and eyes.[1] The motor centres of the head and eyes are—some certainly, while others are less clearly defined—situated in the frontal lobes.

Destruction of the frontal lobes, according to the degree of its completeness, impairs or paralyses the lateral movements of the head and eyes. Though some ocular movements may be excited reflexly by retinal impressions, there appears to be loss of the power of looking at, or directing the gaze towards, objects which do not fall spontaneously within the field of vision. Correlative with this immobility of the head and eyes there is the aspect of uninterest and stupidity, the absence of that active curiosity which is normally manifested by monkeys, and the mental degradation which seems to depend on the loss of the faculty of attention and all that it implies in the sphere of intellectual operations.

The symptoms of lesions and disease of the frontal lobes in man, though not sufficient to establish any positive physiological functional relationships, are, however, in accordance with the negative character of experimental lesions,

[1] Though ptosis has been described by Grasset (*Localisations dans les Maladies Cérébrales*, 1880), and by Landouzy ('Blépharoptose Cérébrale,' *Archives Gén. de Méd.* 1877) apparently in causal relationship with lesions of the angular gyrus in man, we cannot admit any direct causal relationship in face of the total absence of ptosis in cases of experimental destruction of the angular gyrus in monkeys.

unilateral or bilateral, so far as relates to the sensory and motor faculties[1] in general. But several cases have been recorded in which there has been marked intellectual deficiency and instability of character, not unlike those observed in monkeys and dogs.

A comparative study of the relative development of the frontal lobes in different orders of animals renders it abundantly evident that they reach their highest development in man. And the investigations of Huschke,[2] Rudolph Wagner,[3] &c., show that in different races, and in different individuals of the same race, there are great differences in the development of the frontal lobes—a greater development characterising those possessed of the highest mental powers.

In this relation Wagner remarks: 'Among the convolutions of different individuals there are remarkable differences, so that one may distinguish richly convoluted and poorly convoluted brains. These relate only to more numerous divisions and to bendings, &c. of the primary convolutions, which retain the same number and essential position in all normal brains of whatever race. The most notable differences occur in the convolution of the frontal lobes. There are to be found brains of adults which in this respect resemble the brain of a seven months' fœtus, of which it may truly be said that in their outward configuration at least they have remained in a fœtal condition. This slighter development of the frontal convolutions occurs more especially in the female brain, so that it may be said that they resemble in this respect the fœtal brain in its later stages of development before the complete evolution of the frontal lobes. There are to be found also male brains with the same characters, which may therefore be characterised as belonging to the female type; and female brains which in their richness of convolution approach the male type. As a rule, however, the convolutions and sulci are better developed

[1] See the author's *Localisation of Cerebral Disease*, 1878; Charcot et Pitres, 'Localisations dans l'Ecorce des Hémisph.' *Revue Mensuelle*, 1877–78; De Boyer, *Lésions Corticales*, 1879.

[2] *Schädel, Hirn, und Seele*, 1854.

[3] *Morphologie und Physiologie des menschlichen Gehirns als Seelenorgan*, 1860–1862.

in *all* the lobes when the frontal convolutions are specially complex.'[1]

We have therefore many grounds for believing that the frontal lobes, the cortical centres for the head and ocular movements, with their associated sensory centres, form the substrata of those psychical processes which lie at the foundation of the higher intellectual operations. It would, however, be absurd to speak of a special seat of intelligence or intellect in the brain. Intelligence and will have no local habitation distinct from the sensory and motor substrata of the cortex generally. There are centres for special forms of sensation and ideation, and centres for special motor activities and acquisitions, in response to and in association with the activity of sensory centres; and these in their respective cohesions, actions, and interactions form the substrata of mental operations in all their aspects and all their range.

We have not yet found, nor are we likely to discover, any simple formula to express the relation between brain and mind. It is not a mere matter of brute weight or quantity, absolute or relative; though there is no doubt that in animals of the same order a brain below a certain standard of weight is incompatible with normal intelligence. Nor is it merely a matter of quality, by which is meant relative fineness of texture, activity of metabolism, &c.; though such conditions must have an important influence. There may be highly developed sensory centres and defective sensory apparatus, and highly developed motor centres and defective executive apparatus—conditions which must materially influence mental development. But other things being equal—if such a postulate can ever be reasonably made—there are grounds for believing that a high development of certain regions will be found associated with special faculties of which the regions in question are the essential basis. We have seen that in *osmatic* animals, or those possessed of extraordinary faculties of smell, there is a relatively enormous development of the hippocampal lobule, the cortical centre of smell. There can be little doubt that a relatively high development of the visual centres will

[1] *Die typischen Verschiedenheiten der Windungen der Hemisphären u. d. die Lehre vom Hirngewicht*, 1860, p. 89.

be associated with special faculties in the domain of visual sensation and ideation; and similarly in the case of the centres of hearing, touch, and the other sensory faculties.

So we may assume that a high development of special cortical motor centres will be found associated with special motor capacities and powers of acquisition. Special gifts and aptitudes are not, however, incompatible with imbecility or even idiocy. Intelligence and mental power, as a whole, will, however, largely depend on the relative balance or development of one part as compared with another. If, as we have seen reason to conclude, the motor centres are not merely the basis of sensori-motor cohesions and acquisitions, but also the basis of the powers of concentration and control of ideation, we should expect a relatively high development of the motor centres as compared with the sensory centres in those animals and individuals capable of the highest intellectual achievements. That such a relation will be found to exist is more than probable, but on this point and many others, in the absence of rigidly determined data, I forbear further to speculate.

CHAPTER XIII.

CEREBRAL AND CRANIO-CEREBRAL TOPOGRAPHY.

§ 1. In the foregoing chapters, numerous clinical and pathological facts have been adduced, tending to establish the physiological homology of the brain of man with that of the ape, both generally and in respect to individual anatomically homologous parts.

The object of this chapter is to trace these anatomical and physiological homologies in greater detail, and to indicate the relations which subsist between the cerebral convolutions and the surface of the cranium.

In addition to the pathological evidence of the existence of differentiated motor centres in the human brain, supplied by the observations of Hughlings Jackson and others, we have experimental confirmation of the same in the investigations of Bartholow [1] and Sciamanna.[2] Bartholow found, in the case of a patient whose brain was laid bare by cancerous ulceration, that the insertion of needle electrodes, in connection with an induction coil, into the grey matter of the hemisphere in the region of the postero-parietal lobe (fig. 126, P_1), caused convulsive movements of the opposite arm and leg; facts which bear out the results of electrical irritation of this region in the brain of the monkey (fig. 69, 1), which, as has been shown (Chapter VIII.), causes movements of the opposite leg and foot. The results obtained by Bartholow were, however, somewhat complex, owing to the method and the state of the patient not

[1] 'Experimental Investigations into the Functions of the Human Brain,' *Amer. Journ. Med. Sciences*, April 1874.

[2] 'Gli Avversari delle Localizzationi cerebrali,' *Arch. di Psichiatria e Scienze penali*, 1882.

being consistent with the conditions of exact localisation of the stimulus.

Sciamanna, in a case of trephining for fracture of the right parietal bone, applied the electrical stimulus of the faradic, and also the galvanic, current to the surface of the dura mater covering certain regions, defined more accurately *post mortem*. The results thus obtained, though obviously wanting in accuracy, were such as to indicate the existence of centres similar to those defined in the brain of the monkey. Irritation about the middle of the ascending frontal convolution caused action of the masseter muscles. Irritation of the lower third of the ascending parietal convolution caused action of the angle of the mouth and elevation of the ala of the nose and upper lip on the opposite side. Irritation somewhat posterior, in the region of the intraparietal sulcus, caused extension of the left hand, specially of the first three fingers, together with flexion of the forearm and elevation of the eyebrows.

Irritation above the junction of the supramarginal lobule with the superior temporo-sphenoidal convolution caused rotation of the head to the left, movements of the orbicularis palpebrarum, elevation of the eyebrows, and slight movements of protrusion and retraction of the tongue. Notwithstanding the unavoidably diffuse character of the irritation, it is not difficult to discover effects very similar to those resulting from stimulation of areas 8, 9, 10, *a*, 11, 13, and 14, in the brain of the monkey (compare fig. 70, Chapter VIII. with description).

We have thus experimental as well as clinical proof that in the human brain electrical irritation of the region corresponding to the motor zone of the monkey produces similar motor reactions on the opposite side of the body.

§ 2. The brain of man is constructed on the same type as that of the monkey, and essentially the same primary fissures and convolutions are recognisable in both :— the chief differences consisting in the greater complexity of the convolutional arrangement of the human brain, caused by the development of numerous secondary and tertiary gyri, which tend to obscure the simple type of the simian brain. These differences are very marked in the adult and highly developed brain, but are less pronounced in that of the fœtus.

The topography, homologies, and nomenclature of the cerebral convolutions have been investigated by many anatomists. The nomenclature is not altogether uniform. In the following description I have principally followed that of Ecker,[1] which with certain differences, which are indicated, agrees in the main with that of Huxley, Turner, and English anatomists and pathologists.

§ 3. Of the primary fissures or sulci the fissure of Sylvius (fig. 126, s) is easily recognised, and the corresponding fissure, (fig. 127, A) in the brain of the monkey evident. The fissure of Sylvius divides into two rami, the posterior or horizontal (s′) and the ascending or anterior (s″). The portion included between these two branches sometimes receives the name of the *operculum* (Klappdeckel), and forms the roof of the island of Reil. The *fissure of Rolando* (c) or *central sulcus*, corresponds in position and direction with B (fig. 127) in the brain of the monkey.

The *parieto-occipital fissure* (fig. 126, *p o*) corresponds to c (fig. 127) in the brain of the monkey.

§ 4. *The frontal lobe* (fig. 126, F), including the region situated in advance of the fissure of Rolando (c), is divided by secondary fissures into the following convolutions :—F_1, the *superior frontal convolution* ; F_2, the *middle frontal convolution* ; F_3 the *inferior* or *third frontal convolution*.

The sulci, which separate these convolutions from each other, are termed respectively the *supero-frontal* (fig. 126, f_1) and *infero-frontal* (f_2). The sulci *sf* and *if* in the brain of the monkey (fig. 127) were considered by Gratiolet to be homologous with f_1, and f_2 respectively, and the convolutions F_1, F_2, F_3 homologous with the superior, middle, and inferior frontal convolutions of the human brain. But the investigations of Bischoff have rendered this more than doubtful, and shown that with the exception of the anthropoid apes, which possess a more or less distinct ascending ramus of the fissure of Sylvius, and a rudimentary inferior frontal convolution, monkeys in general cannot be said to have a third or inferior frontal convolution. Hence F_1 and F_2 would together form the homologue of the superior frontal (F_1), and F_3 would be homologous

[1] *The Convolutions of the Human Brain* (Galton), 1873.

really with the second or middle frontal convolution (fig. 126, F_2).

The three frontal convolutions terminate posteriorly in a convolution which forms the anterior boundary of the fissure of Rolando, termed the *anterior central, ascending frontal*

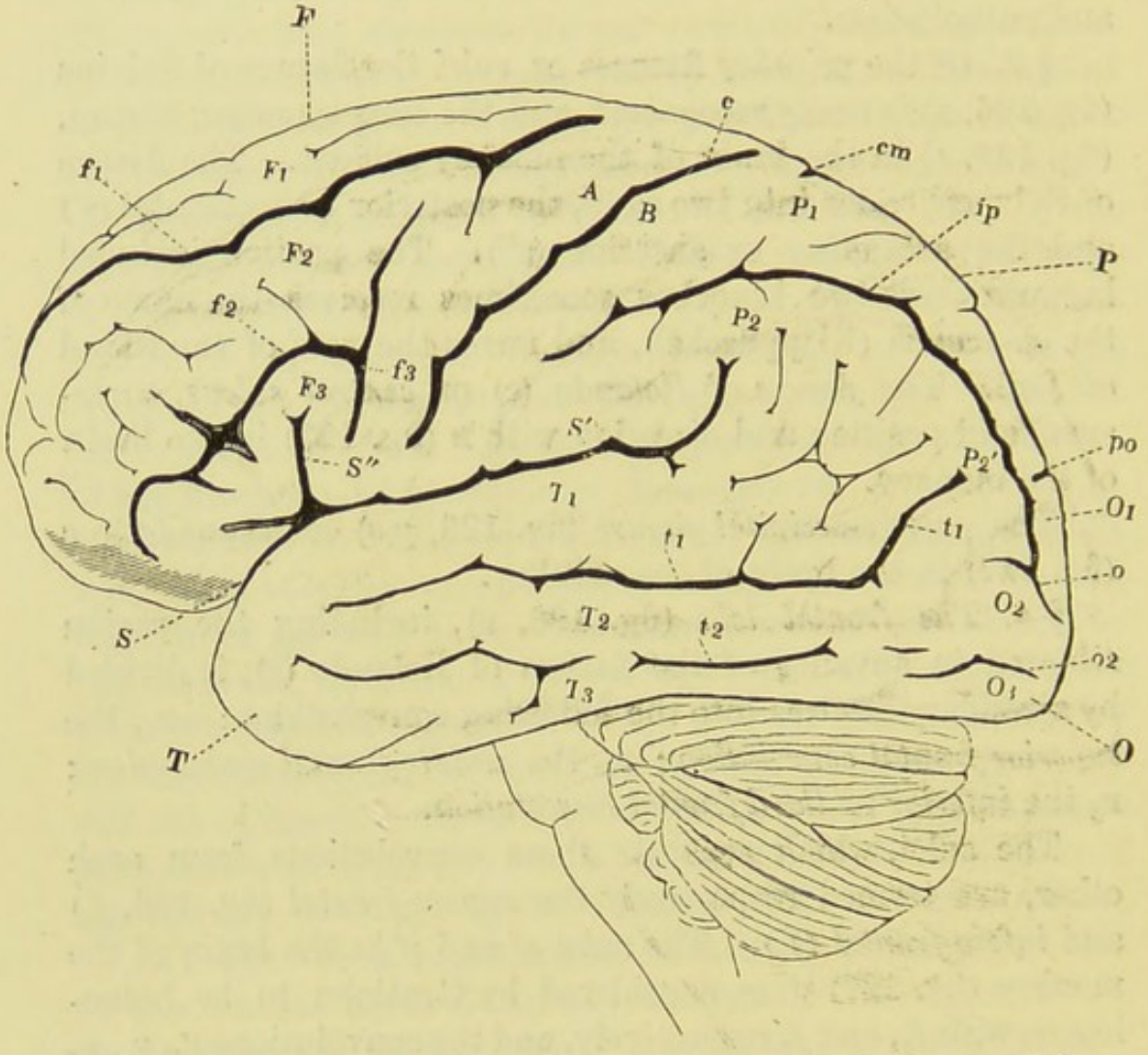


FIG. 126.—Lateral View of the Human Brain (Ecker).—F, frontal lobe. P, parietal lobe. O, occipital lobe. T, temporo-sphenoidal lobe. S, fissure of Sylvius. S', horizontal; S'', ascending ramus of the same. *c*, sulcus centralis, or fissure of Rolando. A, anterior central convolution, or ascending frontal. B, posterior central convolution, or ascending parietal. F_1, superior; F_2, middle; F_3, inferior frontal convolutions. f_1, superior; f_2, inferior frontal sulcus; f_3, sulcus præcentralis. P_1, superior parietal lobule, or postero-parietal lobule; P_2, inferior parietal lobule, viz. P_2', gyrus supra-marginalis; P_2'', gyrus angularis. *ip*, sulcus intraparietalis. *cm*, termination of the calloso-marginal fissure. O_1, first; O_2, second; O_3, third occipital convolutions. *po*, parieto-occipital fissure. *o*, sulcus occipitalis transversus; o_2, sulcus occipitalis longitudinalis inferior. T_1, first; T_2, second; T_3, third temporo-sphenoidal convolutions. t_1, first; t_2, second temporo-sphenoidal fissures

(Turner), or *antero-parietal convolution* (Huxley) (fig. 126, A). The continuity of the three frontal convolutions with the ascending frontal is interrupted by a sulcus termed the *antero-*

parietal sulcus (Huxley), or *sulcus præcentralis* (Ecker) (fig. 126, f_3) corresponding to *a p* (fig. 127) in the brain of the monkey. The ascending ramus of the fissure of Sylvius (s″) likewise partially interrupts the continuity of the inferior frontal convolution with the ascending frontal. This ramus is regarded by Turner as the continuation of the antero-parietal sulcus; but a direct continuity, according to Ecker, is quite an exceptional occurrence. The ascending ramus of the fissure of Sylvius is indicated distinctly only in the anthropoid apes.

The inferior aspect of the frontal lobe is sometimes termed

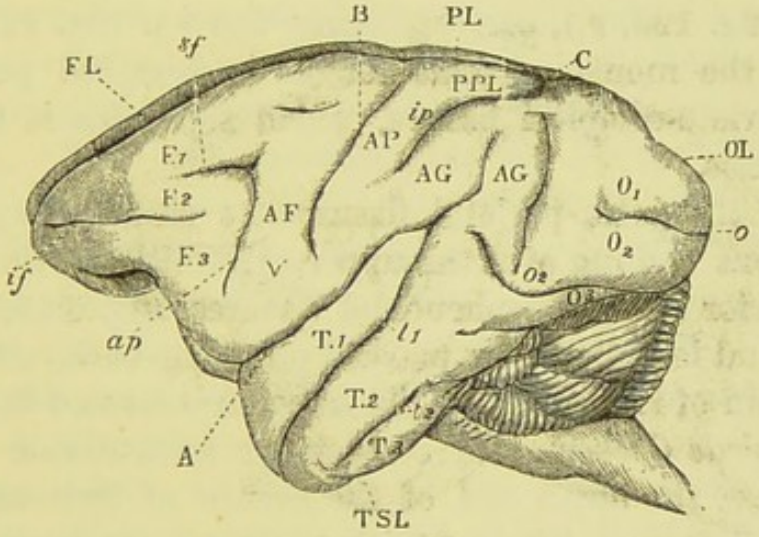


FIG. 127.—Left Hemisphere of Brain of Monkey (Macaque).—A, the fissure of Sylvius. B, the fissure of Rolando. C, the parieto-occipital fissure. FL, the frontal lobe. PL, the parietal lobe. OL, the occipital lobe. TSL, the temporo-sphenoidal lobe. F_1, the superior frontal convolution. F_2, the middle frontal convolution. F_3, the inferior frontal convolution. *sf*, the supero-frontal sulcus. *if*, the infero-frontal sulcus. *ap*, the antero-parietal sulcus. AF, the ascending frontal convolution. AP, the ascending parietal convolution. PPL, the postero-parietal lobule. AG, the angular gyrus. *ip*, the intra-parietal sulcus. T_1, T_2, T_3, the superior, middle, and inferior temporo-sphenoidal convolutions. t_1, t_2, the superior and inferior temporo-sphenoidal sulci. O_1, O_2, and O_3, the superior, middle, and inferior occipital convolutions. *o*, o_2, the first and second occipital fissures.

the *orbital lobule*, from its position in reference to the roof of the orbit (see fig. 17, 2′, fig. 129, F O).

§ 5. *The parietal lobe* (fig. 126, P) is bounded in front by the fissure of Rolando, behind by the *parieto-occipital fissure* (fig. 126, *p o*), and is separated from the temporo-sphenoidal lobe by the horizontal ramus of the fissure of Sylvius (fig. 126, s′).

In this lobe several convolutions are differentiated. The first, which forms the posterior boundary of the fissure of

Rolando, is termed the *ascending parietal convolution* (Turner), *postero-parietal gyrus* (Huxley), or *posterior central convolution* (Ecker) (fig. 126, B), corresponding to A P (fig. 127) in the brain of the monkey. This convolution is bounded posteriorly by a sulcus termed the *intra-parietal sulcus* (fig. 126, *i p*, and also fig. 127).

The part above the posterior extremity of the intra-parietal sulcus, and between it and the longitudinal fissure, is sometimes termed the *superior parietal lobule* (Ecker); by Huxley and Turner it is termed the *postero-parietal lobule*, and is the superior posterior termination of the ascending parietal convolution (fig. 126, P_1), corresponding to P P L (fig. 127) in the brain of the monkey. This lobule is bounded posteriorly by the parieto-occipital fissure, which separates it from the occipital lobe.

Below the intra-parietal fissure are situated a group of convolutions arching over the upper extremities of the Sylvian and superior temporo-sphenoidal fissures (fig. 126, t_1) more complex and less distinctly marked off from each other than in the brain of the monkey. This region is termed the *inferior parietal lobule* (Ecker), and consists of an anterior division, arching over the upper end of the fissure of Sylvius, termed the *supra-marginal lobule*, or *lobule du pli courbe* (Gratiolet) (fig. 126, P_2); and a posterior division, which arches over the upper end of the superior temporo-sphenoidal fissure, and becomes continuous with the middle temporo-sphenoidal convolution (fig. 126, T_2); and is termed the *pli courbe* (Gratiolet), or the *angular gyrus* (Huxley) (fig. 126, P_2'). In the monkey —macaque—there is no clear differentiation of this region into a supra-marginal lobule, and an angular gyrus. The two are represented together in fig. 127, A G, the anterior inferior part of which may be regarded as the homologue of the highly developed supra-marginal lobule in the human brain.

§ 6. *The temporo-sphenoidal lobe* (fig. 126, T) lies behind and below the fissure of Sylvius, which separates it from the frontal and parietal lobes; posteriorly it merges with the occipital lobe, the anterior boundary of which is formed by the parieto-occipital fissure.

The temporo-sphenoidal lobe is divided by two sulci into

three tiers of convolutions. One fissure which runs parallel to the horizontal ramus of the fissure of Sylvius, is termed the *superior temporo-sphenoidal fissure* (fig. 126, t_1), or *parallel fissure* (Gratiolet). Between the fissure of Sylvius and the superior temporo-sphenoidal fissure lies the *superior temporo-sphenoidal convolution* (fig. 126, T_1), or, as it is sometimes termed, the *infra-marginal gyrus*.

Another fissure, running parallel to the superior temporo-sphenoidal fissure, is termed the *middle temporo-sphenoidal fissure* (fig. 126, t_2). Between these two is situated the *middle temporo-sphenoidal convolution* (fig. 126, T_2).

On the inferior aspect of this lobe is another fissure termed the *inferior temporo-sphenoidal fissure*, which forms the lower boundary of the *inferior temporo-sphenoidal convolution* (fig. 126, T_3). The corresponding regions in the brain of the monkey are indicated by the same letters (fig. 127).

§ 7. *The occipital lobe* (fig. 126, o) is not defined anteriorly, except at the site of the parieto-occipital fissure. It fuses with the parietal and temporo-sphenoidal lobes by means of connecting gyri, termed by Gratiolet 'bridging convolutions,' or 'plis de passage.'

Ecker objects to the use of the term 'bridging convolutions,' and gives special names to the convolutions on the lateral aspect of the occipital lobe, as follows:—The *gyrus occipitalis primus* (fig. 126, o_1) connects the occipital lobe with the postero-parietal lobule. It is termed by Gratiolet the *pli de passage supérieur externe*, and *pli occipital supérieur*, and by Huxley, the *first external annectent gyrus*. This convolution is separated from the next by a sulcus termed the *sulcus occipitalis transversus* (fig. 126, o) corresponding to (o), fig. 125, in the brain of the monkey. The next convolution is termed the second occipital, or *gyrus occipitalis secundus* (figs. 126, 127, o_2), or *deuxième pli de passage externe* (Gratiolet), or *second external annectent gyrus* (Huxley). This convolution runs anteriorly into the gyrus angularis. The third occipital convolution, or *gyrus occipitalis tertius* (fig. 126, o_3), runs parallel with the preceding, and joins the third temporo-sphenoidal convolution anteriorly. It is termed by Gratiolet the *troisième et quatrième pli de passage externe*, or *pli occipital inférieur*.

§ 8. On the internal or mesial aspect of the hemisphere the following fissures and convolutions are differentiated.

The convolution immediately bounding the corpus callosum is termed the *gyrus fornicatus* (fig. 128, G*f*), or *callosal gyrus* (Huxley). It commences at the frontal extremity of the brain, beneath the *genu* of the corpus callosum, and moulded on this terminates posteriorly, by a narrow isthmus, in the *gyrus hippocampi* (fig. 128, H) (Huxley's *uncinate gyrus*).

The hippocampal gyrus ends inferiorly in a crotchet-like

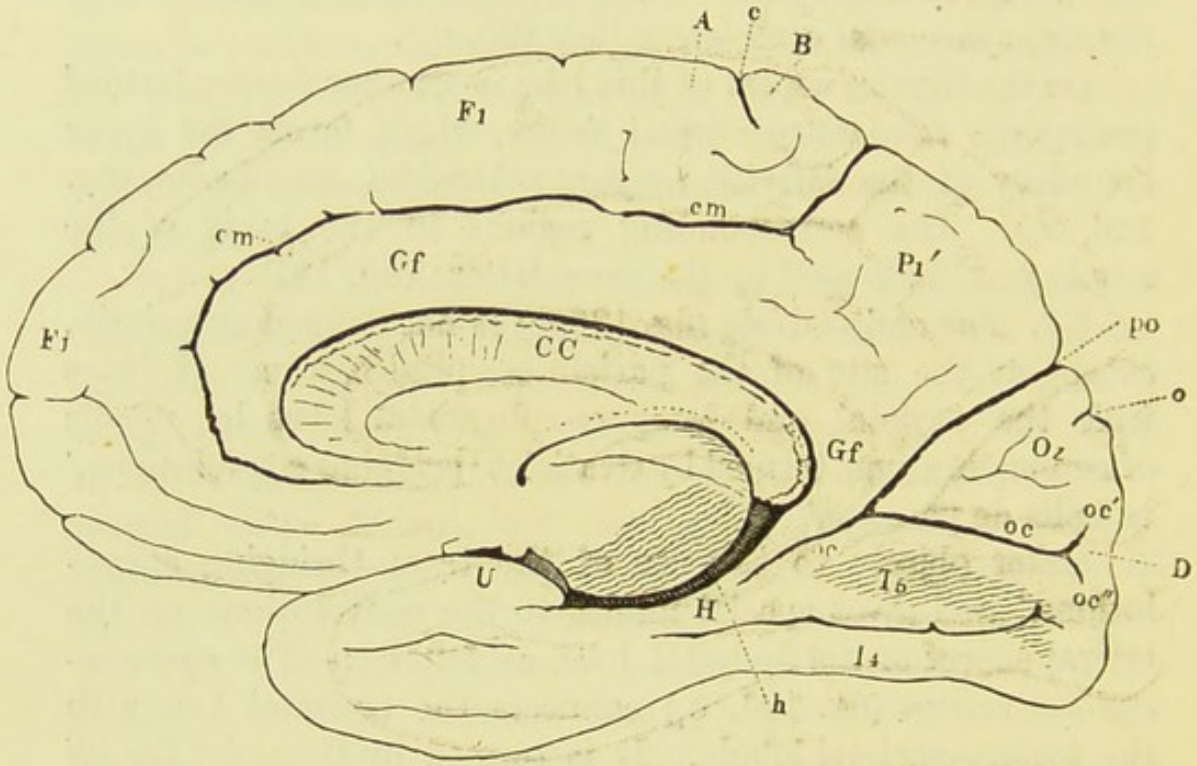


FIG. 128.—View of Median Aspect of Right Hemisphere of Human Brain. (Ecker). —CC, corpus callosum, longitudinally divided. G*f*, gyrus fornicatus. H, gyrus hippocampi. *h*, su cus hippocampi. U, uncinate gyrus. *cm*, su cus calloso-marginalis. F_1, median aspect of the first frontal convolution. *c*, terminal portion of the sulcus centralis, or fissure of Rolando. A, anterior; B, posterior central convolution. P', præcuneus. Oz, cuneus. *po*, parieto-occipital fissure. *o*, sulcus occipitalis transversus. *oc*, calcarine fissure. *oc'*, superior; *oc''*, inferior ramus of the same. D, gyrus descendens. T_1, gyrus occipito-temporalis lateralis (lobulus fusiformis). T_2, gyrus occipito-temporalis medialis (lobulus linguaiis).

extremity termed the *uncus* (fig. 128, U), a part which in some of the lower animals is much more largely developed, and termed the hippocampal lobule. The region of the uncus I have previously described specially as the *subiculum cornu Ammonis*; a term, however, which is sometimes applied to the gyrus hippocampi as a whole. The gyrus fornicatus and gyrus hippocampi together form Broca's *falciform lobe* or *grand lobe limbique*.

Above the gyrus fornicatus, and separated from it by a fissure termed the *calloso-marginal fissure* (fig. 128, *c m*), is a convolution which forms the internal margin of the longitudinal fissure, and has received the name of the *marginal convolution* (fig. 128, F_1). It is merely the mesial or internal aspect of the convolutions of the frontal and parietal lobes. That portion which forms the mesial aspect of the ascending frontal convolution more especially, and bounded posteriorly by the extremity of the calloso-marginal fissure, is often termed the *paracentral lobule*.

Between the posterior extremity of the calloso-marginal sulcus and the parieto-occipital fissure (fig. 128, *p o*) is a lobule,

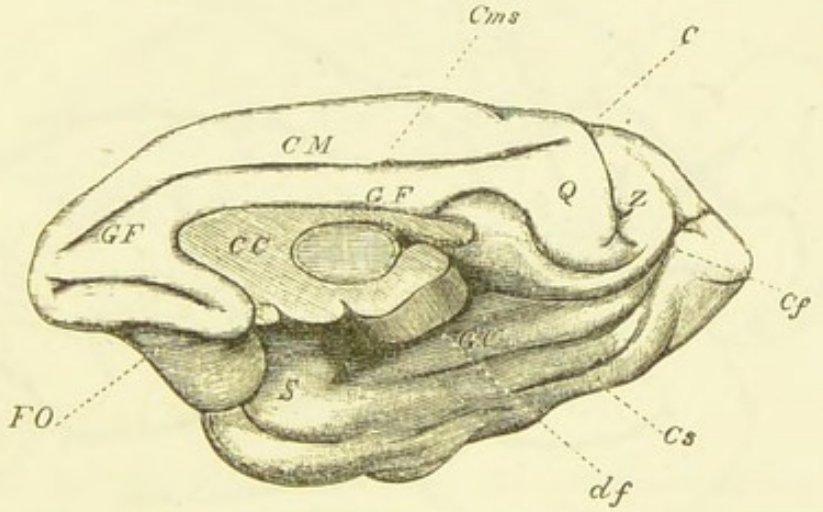


FIG. 129.—Internal Aspect of Right Hemisphere of Brain of Monkey (Macaque).—CC, the corpus callosum divided. C, the internal parieto-occipital fissure. *cms*, the calloso-marginal fissure. *Cf*, the calcarine fissure. *df*, the dentate fissure. *Cs*, the collateral fissure. GF, the gyrus fornicatus. CM, the marginal convolution. GU, the uncinate convolution. S, the crochet, or subiculum cornu Ammonis. Q, the quadrilateral lobule, or præcuneus. Z, the cuneus. FO, the orbital lobule.

of a quadrilateral form, which is the mesial aspect of the postero-parietal lobule. This is termed the *quadrilateral lobule*, or *præcuneus* (fig. 128, P′). Inferiorly, it is continuous with the gyrus fornicatus, though it is to some extent separated by a shallow fissure termed the *subparietal sulcus*. A similar disposition is recognisable in the brain of the monkey (fig. 129, Q, and fig. 72, *s p*).

The fissure *o c* (fig. 128), termed the *calcarine fissure*, marks the position internally of the calcar avis, or hippocampus minor, in the posterior cornu of the lateral ventricle. The parieto-occipital fissure is seen to fuse with this at an acute

angle. The calcarine fissure is not, as in the monkey (fig. 129, *Cf*), continued anteriorly into the *dentate fissure* (fig. 128, *h*), or *sulcus hippocampi*, and, therefore, does not completely interrupt the superficial continuity of the gyrus fornicatus with the gyrus hippocampi. The dentate fissure marks the position of the hippocampus major, or cornu Ammonis, in the descending cornu of the lateral ventricle. In this fissure the *fascia dentata*, *corps godronné*, or *dentate gyrus*, which forms a border to the hippocampus major, is situated.

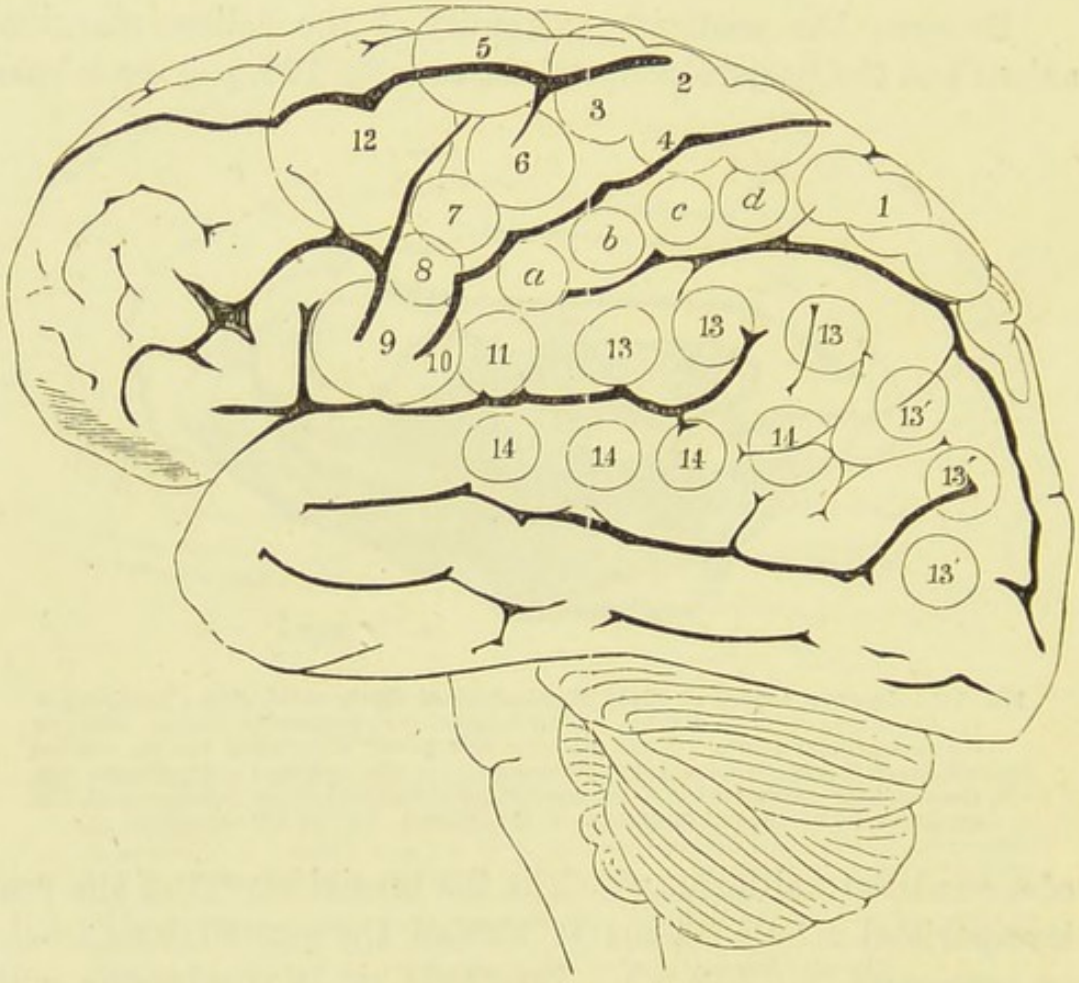


FIG. 130.—Lateral View of Human Brain. The circles and letters have the same signification as those in the brain of the monkey, fig. 131.

Between the parieto-occipital and calcarine fissures a wedge-shaped lobule is marked off on the mesial aspect of the occipital lobe. This is termed the *cuneus* (fig. 128, o *z*), or *internal occipital lobule* (Huxley) (fig. 129, z).

Running along the internal or mesial aspect of the occipital and temporo-sphenoidal lobes is a fissure termed the *collateral*

fissure (Huxley), or *sulcus occipito-temporalis*, which separates two convolutions from each other, which connect the occipital and temporo-sphenoidal lobes with each other, and are, therefore, termed by Ecker the occipito-temporal convolutions (fig. 129, T_4 and T_5). The upper of these is termed the *gyrus occipito-temporalis medialis*, or *lingual lobule* (fig. 128, T_5). The lower, which frequently merges with the inferior temporo-sphenoidal convolution, but at other times is marked off by a fissure, is termed the *gyrus occipito-temporalis lateralis* or *lobulus fusiformis* (fig. 128, T_4). A similar disposition is seen in the brain of the monkey (fig. 129), though the divisions are not so pronounced.

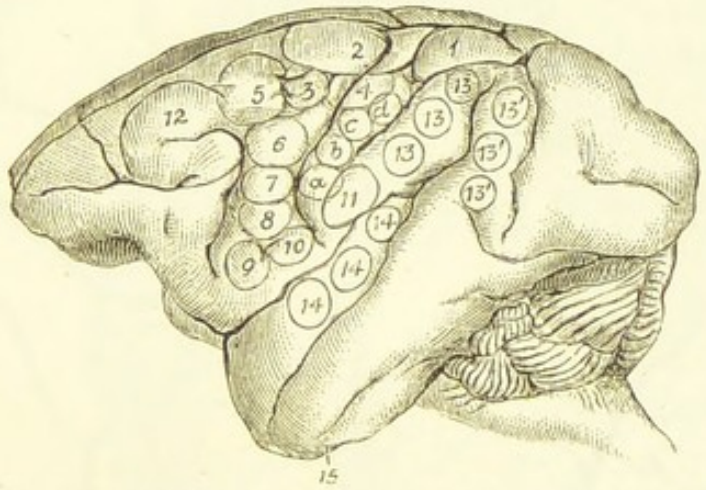


FIG. 131.—Left Hemisphere of Brain of Monkey (see fig. 70 with description).

§ 9. Within the lips of the fissure of Sylvius, and concealed by the *operculum*, or region included between the ascending and horizontal rami of this fissure, lies the central lobe, or island of Reil, which covers the extra-ventricular nucleus of the corpus striatum. Its surface is marked by certain radiating short convolutions, termed the *gyri breves* (see fig. 7, c).

§ 10. In the accompanying figures (figs. 130—133) I have indicated approximately the situation of the centres or areas homologous with those experimentally determined in the brain of the monkey. An exact correspondence can scarcely be supposed to exist, inasmuch as the movements of the arm and hand are more complex and differentiated than those of the monkey; while, on the other hand, there is nothing in man to correspond with the prehensile movements of the lower limbs and tail in the monkey.

In fig. 130 a lateral view of the left hemisphere of the human brain is given, and the same letters placed on regions approximately corresponding to those on fig. 131.

In fig. 132 the upper surface of the human brain is displayed, and the same system followed, to allow of comparison with fig. 133. For the complete details reference is made to Chapter VIII. § 2.

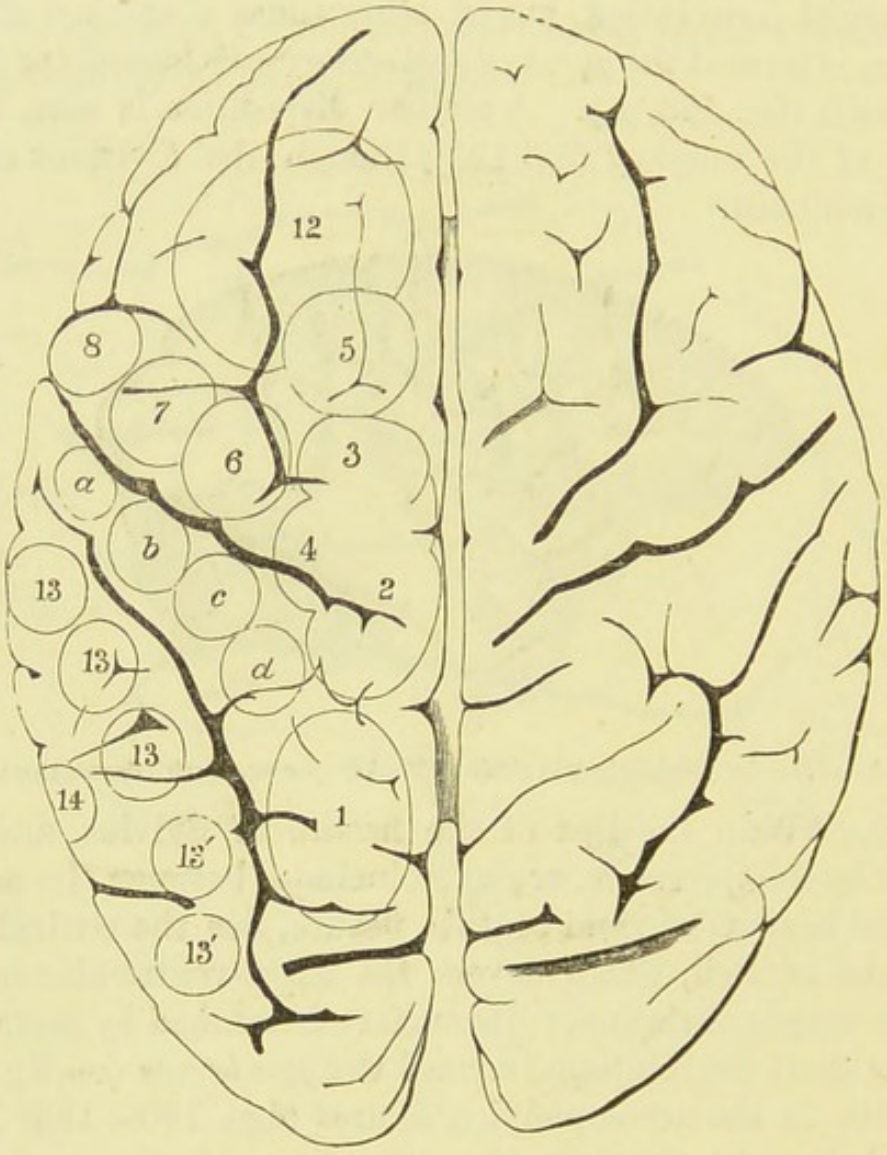


FIG. 132.—Upper Surface of Human Brain. The circles and letters have the same signification as those of Brain of Monkey, fig. 133.

(1), placed on the postero-parietal lobule, indicates the position of the centres for movements of the opposite leg and foot, such as are concerned in locomotion.

(2), (3), (4), placed together on the convolutions bounding the upper extremity of the fissure of Rolando, include centres

for various complex movements of the arms and legs, such as are concerned in climbing, swimming, &c.

(5), situated at the posterior extremity of the superior frontal convolution, at its junction with the ascending frontal, is the centre for the extension forwards of the arm and hand, as in putting forth the hand to touch something in front.

(6), situated on the ascending frontal, just behind the upper end of the posterior extremity of the middle frontal convolution, is the centre for the movements of the hand and

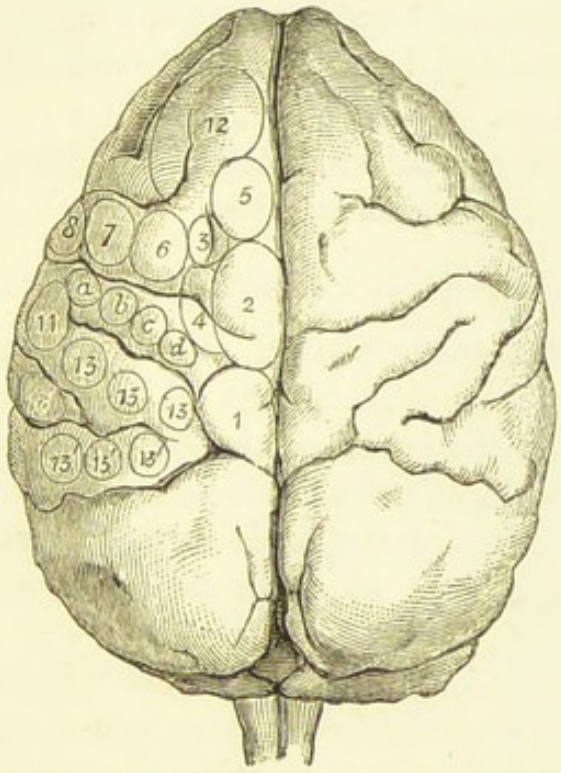


FIG. 133.—Upper Surface of Hemispheres of Monkey.
The circles and included numerals are explained in connection with fig. 69.

forearm, in which the biceps is particularly engaged, viz. supination of the hand and flexion of the forearm.

(7) and (8), centres for the elevators and depressors of the angle of the mouth respectively.

(9) and (10), included together in one, mark the centre for the movements of the lips and tongue, as in articulation. This is the region, disease of which on the left side causes aphasia, and is generally known as Broca's convolution.

(11), the centre of the platysma, retraction of the angle of the mouth.

(12), a centre for lateral movements of the head and eyes, with elevation of the eyelids and dilatation of pupil.

(*a*), (*b*), (*c*), (*d*), placed on the ascending parietal convolution, indicate the centres of movement of the fingers and wrist.

Circles (13) and (13′), placed on the supra-marginal lobule and angular gyrus, indicate the centre of vision, which includes also the occipital lobe.

Circles (14), placed on the superior temporo-sphenoidal convolution, indicate the situation of the centre of hearing.

The centre of smell is situated in the uncus gyri hippocampi or hippocampal lobule (fig. 128, U).

In close proximity, but not exactly defined as to limits, is the centre of taste.

The centre of touch is situated in the hippocampal region (fig. 128, H), and gyrus fornicatus.

Relations of the Convolutions to the Skull.

§ 11. The determination of the exact relations of the primary fissures and convolutions of the brain to the surface of the cranium is of importance to the physician and surgeon, as a guide to the localisation and estimation of the effects of diseases and injuries of the brain and its coverings, and may prove of great service in anthropological and craniological investigations.

Broca's[1] method, followed by Féré,[2] Ecker,[3] &c. consists in driving pegs into the brain at certain fixed points in the sutures of the skull, and estimating the exact distance of the principal fissures from the points so marked. The principal points thus given, the further details can be filled in without great difficulty. Hefftler's[4] method consists in fixing the skull in a determinate position, and taking the projection on a transparent plate successively of the scalp, cranium, and lastly of the exposed surface of the brain. This method requires four different heads in order to obtain a complete view of the whole brain.

None of these methods, however accurate—and that of

[1] *Revue d'Anthropologie*, 1876.
[2] *Bull. Soc. Anat.* 1875; *Revue d'Anthropologie*, 2me série, tome iv.
[3] *Archiv f. Anthropologie*, 1878.
[4] *Ibid.*

Hefftler seems in this respect the best—is capable of practical application in the living like that of Turner.[1] Turner divided the skull into certain areas, and made accurate drawings of the brain underneath, after removal of the skull and portion of the dura mater corresponding to each area.

The following account is founded on Turner's investigations :—

'In conducting an investigation of this kind it is in the

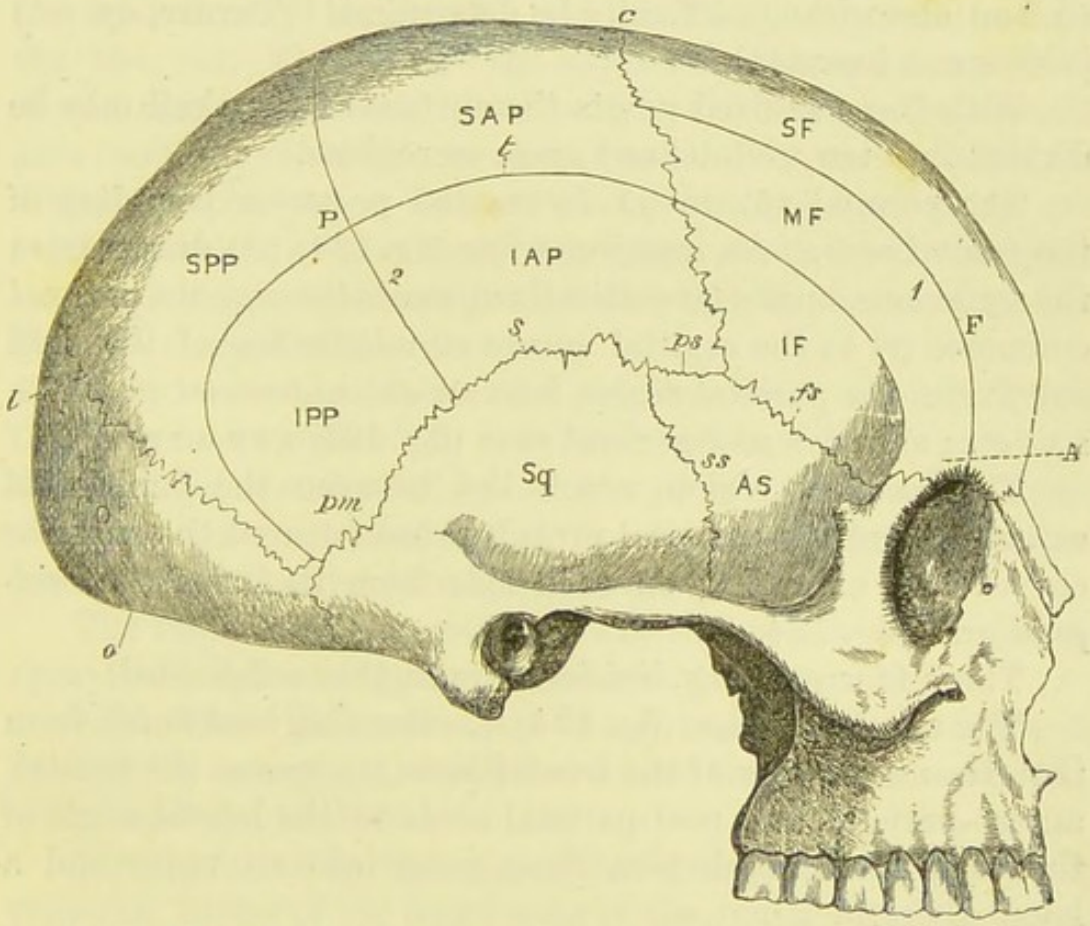


FIG. 134.—Turner's Areas of the Human Skull.—A, the external angular process of the frontal bone. P, the frontal eminence. P, the parietal eminence. *o*, the occipital protuberance. *c*, the coronal suture. *l*, the lambdoidal suture. *s*, the squamous suture. *t*, the temporal ridge. *fs*, the fronto-sphenoid suture. *ps*, the parieto-sphenoid suture. *ss*, the squamoso-sphenoid suture. *pm*, the parieto-mastoid suture. 1, frontal line. 2, parietal line. SF, MF, IF, the supero-, mid-, and infero-frontal subdivisions of the frontal area. SAP, the supero-antero-parietal area. IAP, the infero-antero-parietal area. SPP, the supero-postero-parietal area. IPP, the infero-postero-parietal area. O, the occipital area. Sq, the squamoso-temporal area. AS, the ali-sphenoid area.

first instance necessary to have a clear conception of certain well-defined landmarks, which can be seen or felt when the outer surface of the skull and head are examined. The external occipital protuberance (fig. 134, o), the parietal (P), and

[1] *Journ. Anat. and Phys.*, vols. xiii. and xiv. 1873–1874.

frontal (F) eminences, and the external angular process of the frontal bone (A) are easily recognised structures, the position of which can be determined by manipulating the scalp, and still more readily on the surface of the skull itself. The coronal (*c*) and lambdoidal (*l*) sutures can also be felt through the scalp in most heads, and on the skull itself, the position of the squamous (*s*), squamoso-sphenoid (*s s*), and parieto-sphenoid sutures (*p s*), and the curved line of the temporal ridge (*t*), can also without difficulty be determined' (Turner, *op. cit.*) [references inserted].

With these as fixed points the surface of the skull may be divided into ten well-defined areas or regions.

The coronal suture (*c*) forms the posterior boundary of the *frontal area*. An imaginary line (fig. 134, (*v*)) drawn from the squamous suture (*s*) vertically upwards through the parietal eminence (P) to the sagittal suture or middle line of the skull subdivides the parietal region into an *antero-parietal* (fig. 134, S A P + I A P) and a *post-parietal area* (fig. 134, S P P + I P P).

The occipital region, which lies between the lambdoidal suture (*l*) and the occipital protuberance (*o*), and the superior curved line extending on each side from it, forms the *occipital area* (fig. 134, O).

These four primary divisions are further subdivided.

The temporal ridge (fig. 134, *t*), extending backwards from the external process of the frontal bone (A), across the frontal, antero-parietal, and post-parietal areas to the lateral angle of the occipital bone, divides these areas into an upper and a lower division.

We have thus an *upper* and a *lower frontal area* (S F and I F); an *upper antero-parietal* (S A P) and a *lower antero-parietal area* (I A P); an *upper postero-parietal* (S P P) and a *lower postero-parietal area* (I P P).

§ 12. The boundaries of these areas are as follows:—The *inferior frontal area*, or, as it may also be called, the fronto-temporal area, is bounded above by the temporal ridge, below by the fronto-sphenoid suture, and behind by the coronal suture. The *inferior antero-parietal area* is bounded above by the temporal ridge, below by the squamous and parieto-sphenoid sutures, in front by the coronal suture, and behind by

the vertical line through the parietal eminence. The *inferior postero-parietal area* is bounded above by the temporal ridge, in front by the parietal line above referred to, below by the posterior part of the squamous suture and by the parieto-mastoid suture.

The *upper frontal area*, which includes all the frontal regions above the temporal ridge, is again divided into two, by a line drawn vertically upwards and backwards from above the orbit through the frontal eminence to the coronal suture (fig. 134, (1)). This divides the upper frontal area into a *supero-frontal* (S F) and a *mid-frontal area* (M F). Hence the frontal area has three subdivisions—a supero-, infero-, and mid-frontal division. The *upper antero-* and *postero-parietal areas* are bounded below by the temporal ridge, above by the sagittal suture, and are separated from each other by the vertical line through the parietal eminence.

Eight areas have thus been marked out. The ninth and tenth are more difficult to define, on account of this region of the skull being concealed by the temporal muscle. The areas alluded to are situated below the squamoso-parietal, sphenoido-parietal, and fronto-sphenoidal sutures.

The lines of the sutures naturally divide this region into a *squamoso-temporal* (Sq) and an *ali-sphenoid area* (As).

§ 13. These different areas being marked off, we can now proceed to consider the relation which the fissures and convolutions have to them.[1]

The fissure of Sylvius (fig. 135, S S) commences behind the posterior border of the lesser wing of the sphenoid, and courses upwards and backwards below the greater wing of the sphenoid, where it articulates with the anterior inferior angle of the parietal bone, and then appears in the lower part of the inferior antero-parietal region.

The fissure of Rolando (fig. 135, R) lies in the antero-parietal region, both in its superior and inferior divisions. It is situated at a variable distance behind the coronal suture, Turner finding its upper extremity sometimes as much as two

[1] There are certain variations, as Féré has pointed out, according to sex and age, depending on differences of volume and differences in development respectively. These it is not considered necessary to discuss here minutely.

inches behind the top of the suture, and its lower end as much as an inch and a half behind the lower extremity of the same. Occasionally its upper and lower extremities are not more than 1·5 and 1·3 inch posterior to the extremities of this suture respectively.[1] It will thus be seen that the coronal suture does not correspond to the boundary between the frontal and

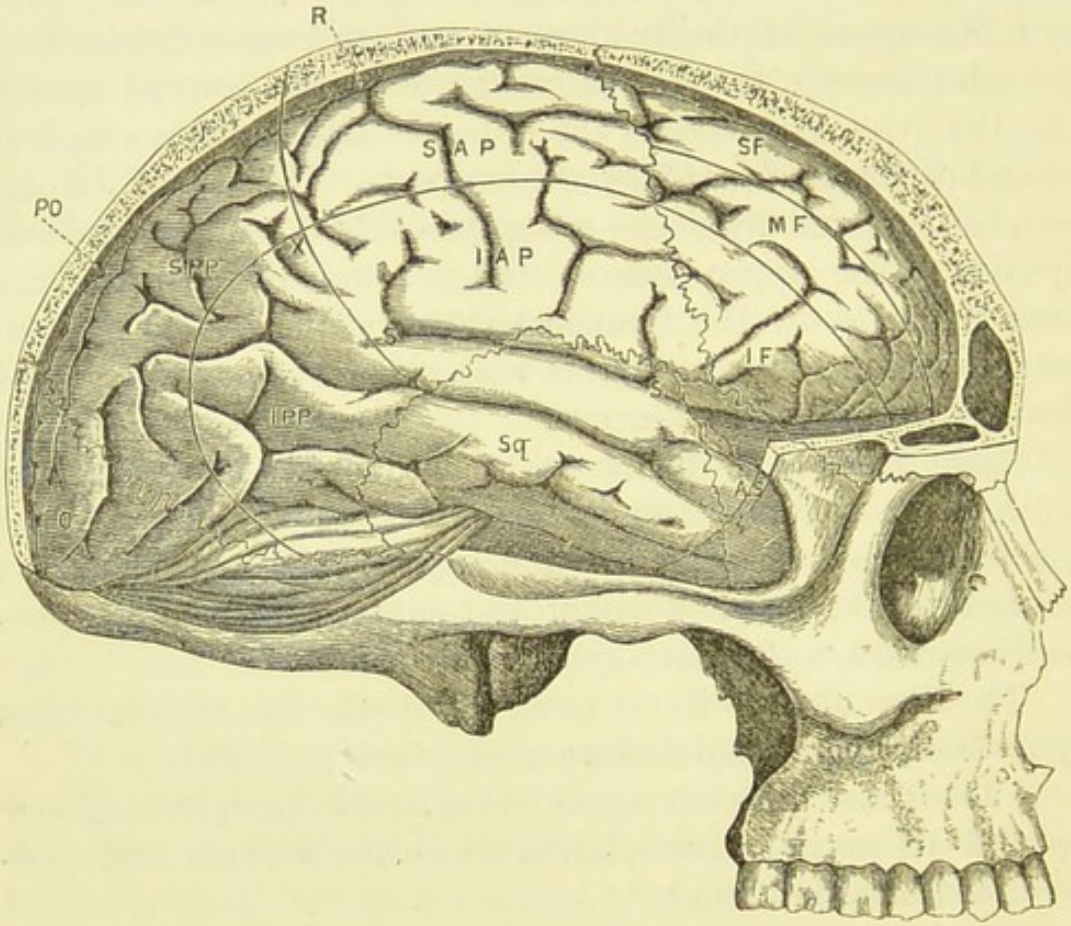


FIG. 135.—Diagram showing the Relations of the Convolutions to the Skull (Turner).—R, the fissure of Rolando, which separates the frontal from the parietal lobe. PO, the parieto-occipital fissure between the parietal and occipital lobes. SS, the fissure of Sylvius, which separates the temporo-sphenoidal from the frontal and parietal lobes. SF, MF, IF, the supero-, mid-, and infero-frontal subdivisions of the frontal area of the skull; the letters are placed on the superior, middle, and inferior frontal convolutions. SAP, the supero-antero-parietal area of the skull: S is placed on the ascending parietal convolution, AP on the ascending frontal convolution. IAP, the infero-antero-parietal area of the skull: I is placed on the ascending parietal, AP on the ascending frontal convolution. SPP, the supero-postero-parietal area of the skull: the letters are placed on the angular convolution. IPP, the infero-postero-parietal area of the skull: the letters are placed on the mid-temporo-sphenoidal convolution. X, the convolution of the parietal eminence, or supra-marginal gyrus. O, the occipital area of the skull: the letter is placed on the mid-occipital convolution. Sq, the squamoso-temporal region of the skull: the letters are placed on the mid-temporo-sphenoidal convolution. AS, the ali-sphenoid region of the skull: the letters are placed on the tip of the supero-temporo-sphenoidal convolution.

[1] Féré found in twenty-eight males the mean distance of the upper extremity from the coronal suture to be 48 millimetres, and of the lower extremity to be 28 millimetres; while in fifty-four females the distances were 45 and 27 millimetres respectively.

parietal lobes of the brain, which, as has been stated, is formed by the fissure of Rolando.

The parieto-occipital fissure is situated on the average about 0·7 to 0·8 inch in advance of the apex of the lambdoidal suture (fig. 135, P O). Féré and Ecker make it almost exactly coincide with the lambda.

§ 14. Next, as regards the contents of the areas.

The *frontal area* is entirely occupied with the frontal lobe, though it does not cover the whole of what is included under the term, inasmuch as the posterior extremities of the three longitudinal frontal convolutions, and the ascending frontal convolution, lie in the antero-parietal area. The regions included in the frontal area correspond pretty nearly to those which give no external response to electric stimulation. They are, according to the hypothesis advanced (Chapter XII. § 16), the motor substrata of the higher intellectual functions.

The subdivisions of the frontal area formed by the temporal ridge, and by the perpendicular drawn from the orbit through the frontal eminence, correspond to the situation of the superior frontal (S F), mid-frontal (M F), and inferior frontal (I F) convolutions.

§ 15. The *upper antero-parietal area* (S A P) contains the upper two-thirds of the ascending frontal (A P) and ascending parietal (S) convolutions, and the origins of the superior and middle frontal convolutions. The former arises from the ascending frontal about 1·2 or 1·3 inch behind the coronal suture; the latter about an inch behind the same line. At the upper posterior angle of the area part of the postero-parietal lobule is visible, and below this part of the supramarginal lobule may appear.

§ 16. The *lower antero-parietal area* (I A P) contains the lower third of the ascending parietal (I) and ascending frontal (A P) convolutions, and the posterior extremity of the lower frontal convolution (Broca's region). The lower frontal convolution arises from the ascending frontal, somewhat less than an inch behind the lower extremity of the coronal suture. At the upper posterior angle of this area a small portion of the supramarginal gyrus is visible, and below this a small portion of the superior temporo-sphenoidal convolution comes into view.

These two areas contain (with the exception of part of the postero-parietal lobule) all the motor centres of the limbs, facial muscles, and mouth. The antero-parietal area, therefore, is specially the motor area of the skull.

§ 17. The *upper postero-parietal area* (fig. 135, S P P) contains the greater part of the postero-parietal lobule. Below it lies the upper portion of the angular gyrus (S P P) and part of the supra-marginal gyrus (x). Posteriorly, what are generally termed the annectent gyri blend with the occipital lobe.

§ 18. The *lower postero-parietal area* (I P P) contains part of the supra-marginal gyrus; behind it, part of the angular gyrus; and, below this, the posterior or upper ends of the temporo-sphenoidal convolutions.

The postero-parietal area taken as a whole, if we except the postero-parietal lobule, corresponds with sensory regions, and particularly with the centres of vision, which occupy a large extent of this area. It might be of importance, in a phrenological sense, to determine whether there is a relation between the development of this region with the next, and those mental faculties of which sight is the basis.

§ 19. The *occipital area* (fig. 135, o) indicates the situation of the occipital lobe, though it does not entirely cover it; inasmuch as part of the occipital lobe generally extends anteriorly beyond the lambdoidal suture into the postero-parietal area.

§ 20. The *squamoso-temporal area* (fig. 135, s *q*) contains the greater portion of the temporo-sphenoidal convolutions, but the superior temporo-sphenoidal convolution (the centre of hearing), though for the most part under cover of the squamoso-temporal and greater wing of the sphenoid, ascends into both the lower antero- and lower postero-parietal areas.

§ 21. The *ali-sphenoid area* (fig. 135, A S) contains the lower or anterior extremity of the temporo-sphenoidal lobe, and, therefore, corresponds to the position of the centres of smell and taste.

§ 22. The central lobe, or island of Reil, does not come to the surface, but lies concealed within the fissure of Sylvius. It is situated behind the upper part of the greater wing of the

sphenoid, and opposite its line of articulation with the anterior inferior angle of the parietal bone and squamous portion of the temporal.

The convolutions situated on the internal aspect of the hemisphere are altogether out of relation to the surface of the skull.

For the guidance of the surgeon, desirous of trephining over a given cortical region, certain rules of measurement have been laid down by Broca, Pozzi, Lucas Championnière, and others. The superior and inferior extremities of the fissure of Rolando, the principal point of orientation, can be determined as follows. A perpendicular line drawn from the external auditory meatus to the middle line of the vertex indicates the position of the *bregma*, or point of intersection of the sagittal and biparietal sutures. The upper extremity of the fissure of Rolando lies 47 to 48 millimetres behind this point. To find the inferior extremity a horizontal line, 7 centimetres in length, is to be drawn from the external angular process of the frontal bone. A perpendicular line is to be raised on the extremity of this line 3 centimetres in height, and the extremity will indicate the position of the lower end of the fissure of Rolando.

Reid [1] has suggested the following rules for determining the position of the principal fissures and convolutions in relation to easily felt landmarks on the skull. These are the glabella or root of the nose, the external occipital protuberance, the superior curved line of the occiput, the parietal eminence, the posterior border of the mastoid process, the depression in front of the external auditory meatus, the external angular process of the frontal bone, the frontal part of the temporal ridge, and the supra-orbital notch (fig. 136 with description). A base line, from which all perpendiculars are drawn, is supposed to run through the middle of the external auditory meatus and the inferior margin of the orbit.

The longitudinal fissure between the hemispheres is indicated by a line from the glabella to the external occipital protuberance, and the transverse fissure is indicated by a line

[1] 'The Principal Fissures and Convolutions of the Cerebrum,' *Lancet*, 1884.

from this same protuberance to the external auditory meatus (fig. 136, B C).

If a point is taken an inch and a quarter behind the external angular process of the frontal bone, and another three-quarters of an inch below the most prominent part of the parietal eminence, the line joining these two points will indicate the position of the fissure of Sylvius. The first three-quarters of an inch from before backwards will indicate the main fissure. From this point the ascending ramus ascends for

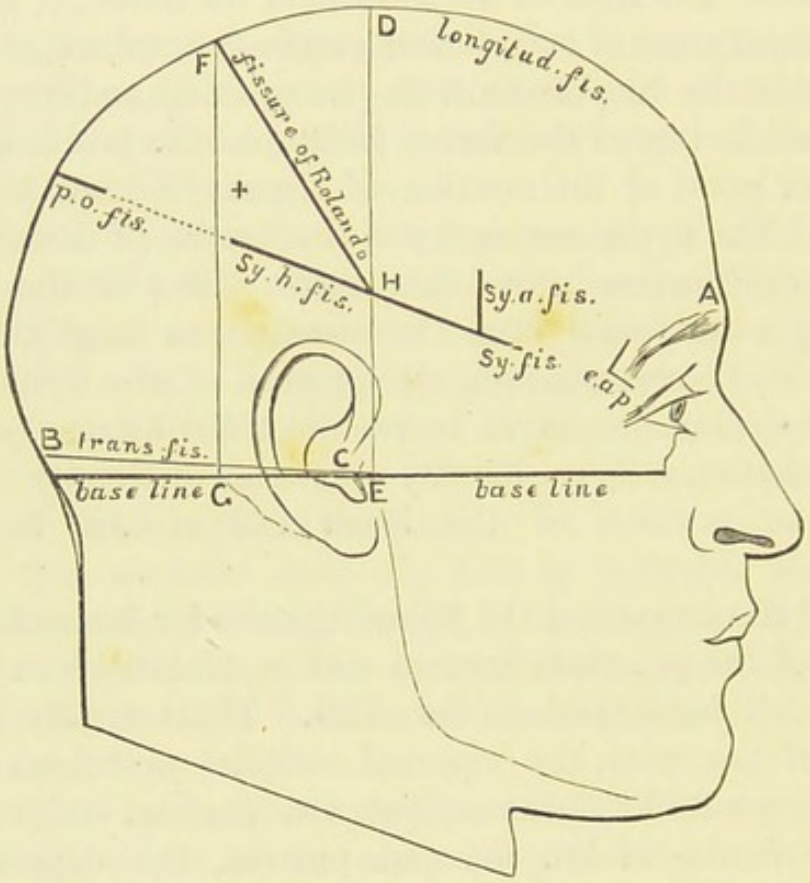


FIG. 136.—Diagram of Cranio-Cerebral Relations (Reid).—A, glabella. B, external occipital protuberance. *e*, *a*, *p*, external angular process of frontal bone. BC, transverse fissure. AB, longitudinal fissure. *Sy. fis.*, Sylvian fissure. *Sy. h. fis.*, horizontal limb of fissure of Sylvius. *Sy. a. fis.*, ascending limb of fissure of Sylvius. DE, perpendicular line from depression in front of external auditory meatus to vertex. FG, perpendicular line from posterior margin of base of mastoid process to vertex. FH, fissure of Rolando. *p*, *o*, *fis.*, parieto-occipital fissure. +, most prominent part of parietal eminence.

about an inch. The rest of the line corresponds with the horizontal ramus (fig. 136, *Sy. h. fis.*). If two perpendiculars are raised from the base line to the longitudinal fissure—the one from the depression in front of the external auditory meatus, the other from the posterior border of the mastoid process—and a diagonal be drawn from the upper posterior

angle to the intersection of the anterior line with the fissure of Sylvius, this diagonal will represent the position of the fissure of Rolando.

The parieto-occipital fissure, somewhat variable, will be indicated approximately by the point where the prolongation of the line of the fissure of Sylvius would intersect the longitudinal fissure (fig. 136, *p. o. fis.*)

The ascending frontal convolution will occupy a space about three-quarters of an inch broad parallel with and in

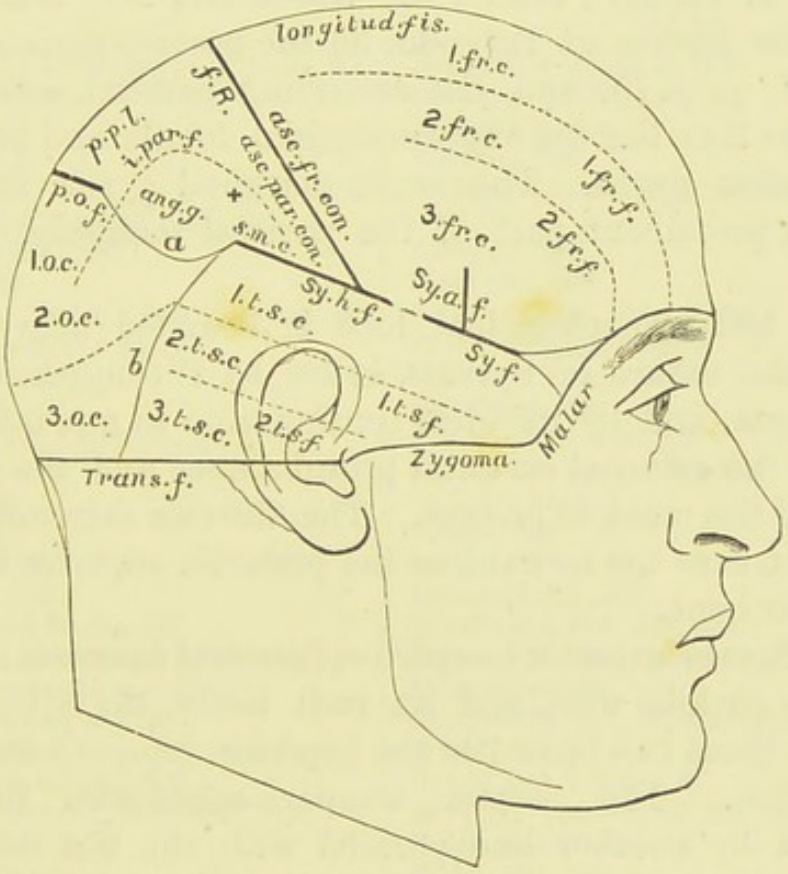


FIG. 137.—Diagram of Cranio-Cerebral Relations (Reid). +, most prominent part of parietal eminence. *a*, convex line forming lower boundary of parietal lobe. 1 *fr. c.*, first frontal convolution. 1 *fr. f.*, first frontal fissure. *f.* R., fissure of Rolando. *Sy. f.*, fissure of Sylvius. *Sy. h. f.*, horizontal limb, and *Sy. a. f.*, ascending limb of Sylvian fissure. *p. o. f.*, parieto-occipital fissure. *i. par. f.*, intra-parietal fissure. *ang. g.*, angular gyrus. *s. m. c.*, supra-marginal convolution. 1 *t. s. c.*, first temporo-sphenoidal convolution. 1 *t. p. s.*, first temporo-sphenoidal fissure. 1 *o. c.*, first occipital convolution. *p. p. l.*, postero-parietal lobule.

front of the fissure of Rolando (fig. 137, *f.* R.). The divisions between the three frontal convolutions will be indicated by lines drawn parallel to the longitudinal fissure, from the supra-orbital notch, and along the frontal part of the temporal ridge respectively to the anterior border of the ascending frontal convolution (fig. 137).

The boundary between the parietal and the occipital and temporo-sphenoidal lobes is somewhat difficult to define. It may be indicated by a curved line, with the convexity downwards, drawn between the end of the parieto-occipital fissure and the end of the Sylvian line (fig. 137, *a*). The intra-parietal fissure is indicated by a line curved in the opposite direction drawn from a point half an inch external to the lower end of the parieto-occipital fissure, and in its anterior third running parallel with the fissure of Rolando, three-quarters of an inch behind it. Above this line, and between it and the fissure of Rolando, lie the postero-parietal lobule (fig. 137, *p. p. l.*), and the ascending parietal convolution. Below the line lies the supra-marginal lobule and portion of the angular gyrus. The supra-marginal gyrus lies under the most prominent part of the parietal eminence (fig. 137, *s. m. c.*).

The temporo-sphenoidal lobe is bounded above by the line of the fissure of Sylvius, below by the upper border of the zygoma, and by its ideal continuation to a point midway between the external occipital protuberance and the posterior border of the mastoid process. The anterior extremity of this lobe extends as far forward as the posterior superior border of the malar bone.

The first or superior temporo-sphenoidal fissure is indicated by a line parallel with, and an inch below, the Sylvian line. Between these two lines lies the superior temporo-sphenoidal convolution. The second temporo-sphenoidal fissure is indicated by another line parallel with the last and about three-quarters of an inch below it. The position of the occipital lobe requires no further special definition.

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