PHILOSOPHICAL TRANSACTIONS.

I. *An Experimental Research upon Cerebro-Cortical Afferent and Efferent Tracts.*

By DAVID FERRIER, *M.D., F.R.S., Professor of Neuropathology, King's College, and* WILLIAM ALDREN TURNER, *M.D., F.R.C.P., Demonstrator of Neuropathology, King's College.*

(*From the Neuropathological Laboratory, King's College, London.*)

Received May 25, 1897,—Read June 17, 1897.

[PLATES 1, 2.]

CONTENTS.

INTRODUCTION.

THE primary object of this research has been to elucidate, by the aid of destructive lesions and the study of consecutive degenerations, the tracts by which impressions of general and special sensibility are conveyed to the cortex of the brain.

Many of the questions treated of in this paper have been the subject of individual investigation by other inquirers, following different methods, such as the histological method of GOLGI; the myelination method of FLECHSIG; the degenerative method after experimental lesions of the brain in some of the lower orders of animals, and in cases of disease in man.

Thus, in respect to the visual system, we have the experimental researches of VON MONAKOW (6), the histological observations of FLECHSIG (8) upon the human fœtus, and the clinicopathological examinations by VIALET (7), DÉJÉRINE (9), and HENSCHEN (2), of cases of disease in man. The conclusions arrived at by these observers, however, are not entirely in accord. HENSCHEN and FLECHSIG are of opinion that the cortical visual area in man is limited to the lips of the calcarine fissure; while VON MONAKOW, VIALET, and DÉJÉRINE assign a more extensive cortical area for this function:—VIALET localising it in the cuneus, lingual and fusiform gyri, and VON MONAKOW on the lateral as well as the mesial surface of the occipital lobe.

A similar divergence of opinion exists as to the relation of the pulvinar thalami and external geniculate body to the cerebral visual tracts. VON MONAKOW and VIALET state that both these ganglia are in direct connection through the optic radiations with the angular gyrus and the occipital lobe; FLECHSIG and HENSCHEN, on the contrary, are of opinion that the external geniculate body alone has a visual function, and that the term "optic radiations" should be limited to that portion of the radiations of GRATIOLET which passes from it to the calcarine fissure.

Recent work on the auditory system includes the experimental researches of VON MONAKOW (22) and BAGINSKY (21); the anatomical investigations of BECHTEREW and FLECHSIG by the myelination method; and the histological observations of HELD (18), and, more especially, of VON KÖLLIKER (17B), by the GOLGI method. It would appear from these researches that fibres of the corpus trapezoides, which continue the cochlear nerve from the accessory auditory ganglion, end partly in the superior olivary bodies, and partly in the posterior quadrigeminal bodies by way of the lateral fillet. Some fibres are, however, continued onwards to the internal geniculate body and optic thalamus of the opposite side. HELD (18), moreover, has described a direct cortical auditory tract ascending from the quadrigeminal region to the first temporal gyrus; and FLECHSIG (8A) has pointed out that the tract which ascends from the internal geniculate body medullates separately from other intra-cerebral systems. DÉJÉRINE (27) has described an efferent tract from the temporal lobe to the upper region of the pons Varolii.

On other corticipetal tracts the most important observations are those of FLECHSIG and HÖSEL (34) upon the cortical continuation of the mesial fillet, and the researches of FLECHSIG (8A) upon the myelination of the several intra-cerebral afferent systems.

In the former, evidence is adduced from a case of disease in man, that the mesial fillet is prolonged from the optic thalamus directly to the cortex of the Rolandic area, and more especially to the posterior portion of this area; while in the latter are described three great systems of corticipetal fibres medullating at different periods, passing from the optic thalamus to the cortex cerebri. These various observations are discussed in detail in the body of the paper.

Our object has been to make a systematic examination by a uniform method—the MARCHI method—of the tracts of degeneration induced by definite lesions of the

sensory tracts or centres in the brain of monkeys, the organisation of whose nervous system most resembles that of man. Thus, on the one hand, the cortical area, supposed to be associated with the representation of the special sense under consideration, was extirpated; on the other hand, the special sensory nerve was divided, or the primary ganglionic structure with which it is connected was destroyed.

In the respective sections into which the paper is divided, the results which we have obtained are compared with those arrived at by other observers, and the points of agreement or difference indicated as well as those on which our own investigations are considered to throw some new light.

The research is divided into two parts :—

1. A physiological part, in which a brief account is given of the symptoms following the lesions; and
2. A histological part, in which the degenerations are described and considered.

SERIES A.

Experiments upon the Visual System.

The portion of the visual system which we have investigated was the cerebral or superior visual segment, consisting of the cortical centres, the optic radiations, and the basal ganglia, viz., pulvinar thalami and anterior quadrigeminal body.

The following experiments were performed :—

1. Extirpation of the occipital lobe (Exps. 1, 2, and 3).*
2. Division of the splenium corporis callosi (Exp. 4).
3. Destruction of the angular gyrus (Exps. 5 and 6).
4. Destruction of the pulvinar thalami (Exp. 7).
5. Extirpation of the frontal lobes along with destruction of the angular gyri (Exp. 8).

It has not been considered necessary to give a detailed account of the symptoms in all the experiments in which operations were performed upon the visual system. In many cases they were merely corroborative of facts now well known, and which do not require repetition.

But as, on some points, there is a want of harmony among the results obtained by different experimenters, it has been deemed advisable to describe those which we have obtained in this research, such, for instance, as the phenomena following *removal of the angular gyrus.*

This convolution was destroyed in two cases. In both animals the removal was complete; but in neither, as demonstrated by post-mortem examination, were the subjacent optic radiations involved.

In both the convolution was destroyed upon the left side. In neither was there

* The numbers refer to the tabular statement of experiments on p. 41.

detected any defect in the movements of the eyeball or levator palpebræ superioris. The only ophthalmoplegic symptom was a temporary dilatation of the opposite pupil. Vision, however, was markedly affected. As soon as the effects of the anæsthetic had passed off, vision was tested in the following manner:—

When the left eye was blindfolded, and the monkey placed upon the floor, it groped about in a manner indicative of total blindness. It invariably came up against obstacles in its way, such as the legs of chairs, and, on reaching the wall, knocked its head against it. When the bandage was removed, it performed the usual antics of a monkey, climbing without difficulty the lattice-work of the cage, and jumping from one object to another. When offered pieces of fruit, it at once seized them, and also picked up portions of apple scattered upon the floor.

These observations were frequently repeated, with exactly the same results. When tested upon the fourth day after the operation in a similar manner, it was apparent, from the behaviour of the animal, that vision was not entirely lost in the right eye. When the left eye was bandaged, the animal seemed to see sufficiently well to avoid knocking its head against the wall or large objects placed in its path, and was also able to jump from a stool to the floor without falling. In other respects no objective phenomena were observed; there was no motor or sensory paralysis, and it could accurately localise a clip attached to any part of its body.

At the end of a week vision of the right eye had further improved. When placed upon the floor, with the left eye bandaged as before, the monkey speedily made off. If it went towards the gas stove, which emitted a bright light, it invariably avoided bumping its head, and lay down in front of the fire. If, on the other hand, it went towards the darker parts of the room, it came up against the wall or other object. It would therefore seem, from this observation, that the animal was not blind in a strong light, such as was given off from the stove, but that it was amblyopic in a dull light.

Later observation showed that a further improvement in the vision occurred in the right eye; for by the end of a month, when the animal was killed in order that the degenerations might be studied, it was able to move about freely in all parts of the room without colliding against obstacles.

The actual extent of the lesion of the angular gyrus is shown in Plate 1, fig. 1.

These observations confirm, what has been elsewhere (1) described, that in the Macaque monkey destruction of the angular gyrus is followed by temporary blindness or amblyopia of the opposite eye; and that this lesion does not cause any ophthalmoplegic defect.

As is well known, removal of the frontal lobe is not followed by any ocular paralysis beyond a temporary inability to move the eyes conjugately to the side opposite the lesion; and, as destruction of the angular gyrus is entirely negative in this respect, an experiment was planned with a view to localise, if possible, the portion of the cortex cerebri in which these movements have their seat. With this

object, the *frontal lobe and angular gyrus were removed* first on one side and then on the other. Immediately after the first operation on the left side, there was conjugate deviation of both eyes to the same side, but no ptosis.

As regards vision it was apparent, from all the usual tests, that the animal was blind in the right eye, and hemiopic to the right in the left eye; while in addition there was anæsthesia of the right side of the body. Five days later the animal was seen to move its eyes conjugately to the right up to, but not beyond, the middle ocular position. By this time the condition as regards vision had altered. It was no longer blind in the right eye, but each eye was hemiopic to the right; objects such as pieces of fruit being picked up from the floor only when placed to the left side. It was never seen to turn its eyes to the right, but this may have been owing to the defect of vision to this side.

Owing to the deviation of the eyes to the left, the animal invariably turned towards this side, the visual field to which seemed to be of normal extent. These symptoms continued without alteration until the end of the third week after the operation, with the exception that it was seen to move both eyes to the right when its attention was drawn to this side by sounds. At this date the monkey was again anæsthetised, and *the right frontal lobe and right angular gyrus removed.* The effect of this operation was to render the animal absolutely blind. There was no evidence, to all the usual tests, of the existence of any visual perception. As regards motility, there was no ptosis, nor were the opening or closing movements of the lids in any way affected. The head and eyes were deviated to the right; both pupils were dilated, but reacted to light. As the monkey was somewhat apathetic, it was difficult to determine accurately the condition as to sensation, but there was no evidence of tactile sensibility on either side, although it responded to pricking and pinching the fingers and toes upon both sides. The monkey was killed upon the fifth day after the second operation without any obvious change having occurred in the symptoms.

The *autopsy* revealed that both frontal lobes and both angular gyri had been destroyed, the frontal lobe and angular gyrus being rather more extensively removed on the left side. The condition of the cerebrum is shown in Plate 1, fig. 2.

The facts quâ ocular movements as ascertained from this experiment indicate :—

1. That both frontal lobes may be removed without any impairment in the movements of the eyeballs other than a temporary inability to turn them to the side away from the lesion;
2. That in addition to the frontal lobes the angular gyri may be removed without any further impairment in the movements of the eyes or of the eyelids.

The influence of the lesion upon vision will be considered after the experiment of destroying the pulvinar thalami has been described.

Some further facts upon the symptoms following removal of the frontal lobes are given in the section devoted to the frontal and pre-frontal systems (Series E).

Destruction of the Pulvinar and Adjacent Portions of the Optic Thalamus.

In this case the operation was performed by removing a considerable portion of the skull upon the left side; the left cerebral hemisphere was carefully retracted so as to reveal the corpus callosum; the posterior half of this structure was divided, and the lateral ventricle opened, so as to expose the dorsal portion of the optic thalamus and pulvinar. These were destroyed by the galvano-cautery. That this was performed without any obvious implication of adjoining structures, such as the internal capsule, optic radiations, or external geniculate body, is evident from the examination of a section (Plate 2, fig. 6) made through the lesion.

The symptoms in the sphere of vision after this operation were as follows:—blindness in the right eye and hemianopsia to the right side in the left eye. This fact was detected by the usual tests and repeatedly confirmed. In addition to this, there was anæsthesia and loss of the power of localising a clip all down the right side.

When again tested five days later, the right eye was no longer blind, but hemiopic, so that there was now homonymous hemianopsia to the right side, with blunting of sensibility and loss of the power of localising a clip down that side of the body.

It may be here mentioned that the temperature was taken in both groins, immediately after the operation and on several subsequent occasions, without any increase above normal being observed.

A month later the monkey remained *in statu quo* as regards vision, being absolutely hemiopic to the right side, but the anæsthesia and inability to localise a clip had given place to merely blunting of cutaneous sensation and defective sense of localisation.

Two months after the operation, when the animal was killed, it was still completely hemiopic to the right side.

A more detailed examination of the lesion showed that the posterior part of the optic thalamus had been almost completely destroyed. There was no evidence in any of the sections that the posterior part of the internal capsule, the optic radiations, or the external geniculate body were implicated. The lesion was limited accurately by the middle line. The splenium corporis callosi had been divided, as shown in the photograph, Plate 2, fig. 6, but there was no other obvious implication of the cerebral hemispheres.

From this experiment some important inferences may be drawn. It has been elsewhere (1) stated that a unilateral lesion involving the whole cortical visual sphere, viz., occipital lobe and angular gyrus, is productive of complete hemianopsia to the opposite side. In this experiment it has been shown that unilateral destruction of the pulvinar thalami is followed by temporary blindness of the opposite eye and hemianopsia in that on the side of lesion; the blindness of the opposite eye being due to hemianopsia plus amblyopia of the whole field, the former being revealed when the latter has passed away.

The phenomena quâ vision following destruction of the pulvinar thalami therefore indicate that the corticipetal fibres both to the occipital lobe and to the angular gyrus pass through this structure. The external geniculate body in this case appeared to be quite intact, yet the degenerations (*vide* p. 24) passed both to the occipital lobe and the angular gyrus.

Degenerations consequent on Lesions of the Cerebral Segment of the Visual System.

The method which has been adopted to trace the secondary degenerations in this research was the osmium-bichromate method of Marchi. The method is not free from fallacy, for a more prolonged experience has confirmed us in the view that the mere existence of black dots throughout a section, or in a limited portion of it, is not altogether indicative of the presence of secondary degeneration. This is established by the presence throughout a series of sections, when the fibres have been cut in a longitudinal direction, of a constant strand or strands of large black bullæ, more especially if these occupy the position of tracts of fibres whose existence has been determined by other means. But the Marchi method is capable of demonstrating the presence of degeneration in single nerve fibres, which is possible by no other method.

(a) *Degenerations following Removal of the Occipital Lobe.*

In these cases the knife was carried along the fissure on the external aspect of this region, which corresponds in position to the external parieto-occipital fissure—the so-called *Affenspalte*; and the whole of the non-convoluted lobe lying posterior to this was removed. This included the cuneus, the convexity of the occipital lobe, the lingual lobe, and the whole of the calcarine fissure with the exception of its anterior extremity, which is prolonged towards the hippocampal fissure.

This operation was followed by a well-marked degeneration through the optic radiations. Reaching the retrolenticular part of the internal capsule, these degenerated fibres passed in a series of large well-defined bundles partly into and partly through the pulvinar, whence many were traced into the outer portion of the anterior quadrigeminal region. A few were traced onwards from this into the so-called "middle zone" of white matter (Plate 2, fig. 5), some of which crossed the middle line into the corresponding body of the opposite side. In the upper parts of this region, some of the fibres coming from the pulvinar were also observed in the posterior commissure, by which means a connection was effected with the opposite side. That the cortical origin of these fibres was limited to the occipital lobe was apparent from the fact that no such strand of degeneration was observed after removal of the angular gyrus.

In addition to these large degenerated bundles of fibres, the external geniculate body and the posterior part of the optic thalamus showed an extensive amount of diffuse scattered degeneration. That this was of the nature of an ascending rather than a Wallerian degeneration might be inferred from the absence of large bullæ of broken-up myeline, the cut surface of these structures being covered with numerous fine black dots.

Microscopic examination of the opposite occipital lobe in these cases revealed the existence of degenerated fibres. These occupied a definite position in the centre of the lobe, viz., in that portion of the central white matter which is formed by the fibres of the forceps corporis callosi. But, as the presence of this degeneration was more clearly seen in the experiment in which the splenium was divided, its description is given in the next section.

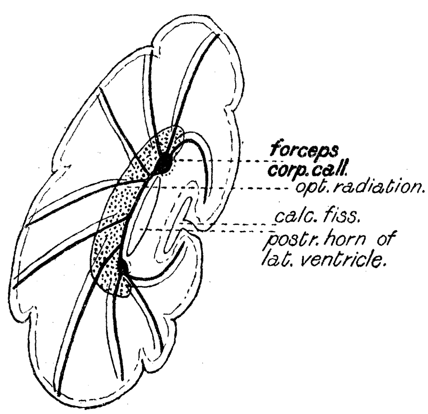
The presence of scattered degenerated fibres in the internal capsule, pes cruris, tegmentum, and spinal cord, which have been described by SHAW and THOMPSON (3), was not confirmed in our experiments.

(b) *Division of the Splenium Corporis Callosi.*

This structure was exposed by gently drawing aside one cerebral hemisphere after removal of a considerable portion of the skull.

The situation of the callosal fibres and their position relatively to the optic radiations, and other fibres in the occipital medulla, agrees with the description

Schema 1.
Frontal section through the occipital lobe.



The radiating thin lines are optic radiations. The radiating thick lines are callosal fibres.

given by SACHS (4). At either pole of the posterior horn of the lateral ventricle in frontal sections there is situated a cup-shaped mass of fibres, joined together along the external wall of the ventricle, which two masses of fibres and the intermediate connection form the occipital prolongation of the forceps corporis callosi. External

to these lie the optic radiations. Lying outside these, again, in man is the stratum sagittale externum, or inferior longitudinal bundle, which is not present in the Macaque brain. Forming the remainder of the occipital medulla, and therefore in the monkey separating the optic radiations from the cortical grey matter, is the stratum proprium occipitale, formed chiefly of commissural fibres, but through which pass the fibres from the forceps callosi and the optic radiations outwards on their way to the occipital cortex (*vide* Schema 1).

Division of the splenium corporis callosi was followed by degeneration of the fibres of the forceps in the position above named, viz., at either pole of the lateral ventricle in frontal sections (Plate 2, fig. 2), and in the narrow strip of white matter joining these two parts along the external wall of the posterior horn, from which it is only separated by the ependyma ventriculi. We have been able to trace the degenerated callosal fibres from this position into both lips of the calcarine fissure, as well as into the cuneus, the external occipital convolutions, and the angular gyrus. These fibres reach the cortex through the central part of the white matter which forms the core of the gyri. As this is the locality also occupied by the fibres of the optic radiations, these two systems of fibres intermingle in their passage from the positions they occupy in the central parts of the lobe to the cortex of the occipital lobe (*vide* later, p. 12).

(c) *Destruction of the Angular Gyrus.*

In the two experiments upon this region here described, special care was taken to avoid injury to the subjacent optic radiations, and these were found intact on subsequent microscopic examination in both cases.

The most obvious degeneration following this operation was found amongst the fibres of the splenium corporis callosi. This was traceable into the white matter of the opposite cerebral hemisphere, but there was no clear evidence of it in the medullary core of the angular gyrus of the opposite side. In the corpus callosum, the degeneration occupied the outer limb of the forceps, or that portion of the callosal body which passes to the outer side of the posterior horn. This observation upon the commissural connexions of the angular gyri is incomplete; but that such a connexion exists between the gyri of opposite sides was further shown by the case in which the splenium corporis callosi was divided, for here a marked degeneration was observed passing into the angular gyrus in the position assigned by SACHS to the callosal fibres. This corresponds with MURATOFF'S (5) experiments upon removal of the cortical motor areas and section of the corpus callosum, inasmuch as division of the corpus callosum showed a more extensive degeneration than that following removal of the cortical area alone.

From this it is evident that the angular gyri, as well as the occipital lobes, are commissurally connected by way of the splenium corporis callosi.

There was no degeneration of those fibres which have been already described as passing from the occipital lobe, through the pulvinar, into the anterior quadrigeminal body.

As the adjacent convolutions—viz., the superior temporal, superior parietal, and occipital gyri—showed evidence of considerable degeneration, it is evident that they are connected with the angular gyrus by association fibres. The degeneration in the occipital lobe was limited to that portion of the occipital medulla which lies outside the optic radiation—the stratum proprium occipitale.

There was no clear evidence of corticifugal fibres passing from the angular gyrus to the basal ganglia; but that this gyrus is connected with the pulvinar by corticipetal fibres will be shown in the next section.

(d) *Destruction of the Pulvinar Thalami.*

The degenerations following destructive lesion of the optic thalamus are numerous and important, and will be treated more fully in subsequent sections, but reference is made here only to those which were traced into the occipito-angular region from destruction of the pulvinar.* In this experiment, the external geniculate body and its radiations were not wounded. Microscopic examination of the occipital lobe on the same side as the lesion of the pulvinar showed well-marked and extensive degeneration in the optic radiations.

The optic radiations in the occipital lobe, as above described, form a large semilunar cap of closely packed fine nerve fibres upon the external aspect of the posterior horn of the lateral ventricle, from which it is separated by a thin band of callosal fibres (*vide ante*). From either end, in frontal sections, there were traced numbers of degenerated fibres, which passed into both lips of the calcarine fissure; but the degeneration was not limited to this portion of the lobe. Given off from the lateral aspect of the radiation were fibres which passed through the stratum proprium into all the external occipital convolutions and into the angular gyrus, which fibres were traced right up to the under-surface of the cortical grey matter in these positions.

The distribution of the pulvinar fibres in the occipital lobe and angular gyrus is therefore seen to coincide with that of the fibres of the corpus callosum and those of the optic radiations.

If the fibres of the optic radiations proper are limited in their distribution to the lips of the calcarine fissure, as FLECHSIG (8) and HENSCHEN (2) conclude, it is evident from our experiments that the pulvinar fibres have a similar termination. Others, however, were found to terminate, not only here, but in all the external occipital convolutions, and also in the angular gyrus.

* On p. 30 will be found a more complete investigation of all the fibres radiating from this region after examination by the MARCHI method.

Reviewing the results obtained by the method of degeneration in conjunction with the symptoms observed during life, it may be stated that the cortical visual area in the Macaque monkey is not limited to the occipital lobe, nor to any special part of this lobe, but to an area which includes the angular gyrus, and may be called the occipito-angular region.

Connecting this area with the basal ganglia are two sets of fibres, which degenerate in opposite directions, one a *corticifugal* system, connecting the occipital lobe with the pulvinar and anterior quadrigeminal bodies; the other a *corticipetal* system, passing from the external geniculate body and pulvinar thalami to the cortex of the occipito-angular region. We have pointed out that the former system has no direct connexion with the angular gyrus, for destruction of this area was not followed by any such efferent degeneration. The existence of an efferent tract of this nature was pointed out by VON MONAKOW, who observed atrophy of the white matter of the middle zone of the anterior quadrigeminal tubercle as a result of destruction of the occipital lobe—an observation which has since been confirmed by others.

This corticifugal system does not form a definite bundle in the optic radiations, but appears as a series of scattered fibres. On reaching the external boundary of the pulvinar thalami the fibres form a number of well-marked fasciculi, some of which end in this structure, but others are continued through it to the outer part of the anterior quadrigeminal region, into which they are capable of being traced, as already described (Plate 2, fig. 5).

Upon the distribution of the corticipetal fibres much diversity of opinion exists.

The observations of VON MONAKOW (6) and VIALET (7) show that the mesial surface of the occipital lobe stands in relation with the posterior and external parts of the pulvinar and external geniculate body, while the external occipital convolutions and angular gyrus are similarly related to the superior part of the pulvinar by means of the upper portion of the optic radiations, facts upon which is based the conclusion that the optic radiations emerge from both the pulvinar thalami and external geniculate body, both of which ganglia are therefore in direct relation with the cortical visual area. The observations of FLECHSIG and HENSCHEN, on the other hand, are opposed to this view. FLECHSIG (8), working by the myelination method, has recently stated that the term "optic radiations" should be limited to the efferent fibres of the external geniculate body, which he has traced to VICQ D'AZYR's line in the lips of the calcarine fissure; while the upper parts of the optic radiations of GRATIOLET are formed by the fibres from the pulvinar to the angular gyrus. He, however, does not consider that the pulvinar thalami forms an internode in the visual system in man, although it receives a large bundle of fibres from the external geniculate body.

HENSCHEN (2) places the visual centre in the lips of the calcarine fissure from the following reasons:—First, in old-standing cases of unilateral destruction of the eyeball atrophy of this part of the cortex was found; secondly, in a case of softening

involving the external geniculate body entirely, and partly also the internal geniculate body and ventral part of the pulvinar, degeneration was traced through the ventral part of the optic radiations to the calcarine fissure ; and thirdly, from the existence of hemianopsia in a case in which an area of softening was limited to the lips of the calcarine fissure.

Our observations tend to confirm the views of VON MONAKOW and VIALET rather than those of HENSCHEN and FLECHSIG.

Destruction of the pulvinar thalami, without any interference with the integrity of the external geniculate body or optic radiations, gave rise to permanent hemianopsia ; while the secondary degenerations of a corticipetal nature were as well marked and as extensive in the angular gyrus as in the occipital lobe ; and, moreover, this degeneration was as evident in the external occipital convolutions as in the cuneus and the lips of the calcarine fissure. This degeneration reached the cortical areas by way of the optic radiations, as described.

On the other hand, it may be contended that these fibres form merely the occipital segment of the great thalamo-cortical system, other portions of which will be described in the sequel.

Although no certain evidence can be obtained from clinicopathological observation in man regarding the existence of visual fibres in the pulvinar thalami, and although FLECHSIG and HENSCHEN state that the optic radiations proper have no direct thalamic connexion, but arise from the external geniculate body alone, we would point to our experiment in which unilateral destruction of the pulvinar thalami gave rise to crossed amblyopia and subsequent permanent hemianopsia, and was followed by well-marked degeneration in both lips of the calcarine fissure and in the angular gyrus. It would, therefore, seem impossible to deny the existence of a visual function to the pulvinar in the Macaque. Moreover, in one of VIALET'S cases of hemianopsia due to softening (Obs. 1) affecting the anterior portion of the cuneus and calcarine fissure, the atrophy was traced as clearly in the pulvinar as in the external geniculate body.

The *commissural connexions* between the occipital lobes are well defined by our experiments. These have been described in part by DÉJÉRINE (9) and VIALET (7) in so far as they affect the splenium and the forceps corporis callosi in man ; but, so far as we are aware, their course and termination in the opposite lobe have not been previously described in detail.

As already stated in the description of this degeneration, the occipital commissural fibres may be traced into the forceps callosi of the opposite side (Plate 2, fig. 2), from which they are again given off to the occipital gyri, and to the lips of the calcarine fissure ; and we have found that these fibres have the same distribution as the thalamic fibres. The angular gyri are also commissurally connected through the splenium.

These observations, and more especially those having reference to the commissural

connexions of the gyri of the calcarine fissure, are at variance with those of BEEVOR (10), who was unable to trace fibres from any part of the corpus callosum to the cortex bounding the calcarine fissure in the marmoset.

The following is a *summary* of the conclusions based upon the preceding observations :—

1. The occipito-angular region is the cortical visual centre.
2. Unilateral destruction of this region, or of the pulvinar thalami, leads to temporary blindness of the opposite eye and persistent homonymous hemianopsia to the opposite side.
3. A corticifugal tract passes from the occipital lobe to the pulvinar thalami and anterior quadrigeminal bodies, more especially on the same side.
4. The corticipetal degenerations following lesion of the pulvinar thalami are traceable to the angular gyrus and occipital lobe, in which lobe the degeneration is as well marked in the external convolutions as in the cuneus and the lips of the calcarine fissure.
5. The angular gyri and occipital lobes are commissurally connected through the splenium and forceps corporis callosi.

SERIES B.

EXPERIMENTS UPON THE AUDITORY SYSTEM.

This system has been studied from the point of view of degeneration by means of the following experiments :—

a. Section of the eighth nerve distal to the auditory ganglion (Exps. 9 and 10).
b. Section of the eighth nerve proximal to and including the auditory ganglion (Exps. 11 and 12).
c. Unilateral destruction of the posterior quadrigeminal body (Exp. 13).
d. Unilateral destruction of the internal geniculate body, including the adjacent part of the tegmentum (Exps. 14 and 15).
e. Destruction of the superior temporal gyrus (Exps. 16 and 17).
f. Amputation of the flocculus cerebelli (Exps. 18 and 19).

In order to reach the auditory nerve and its accessory ganglion, it was necessary to divide the pedunculus flocculi. As in our earlier experiments upon this nerve the degenerations secondary to the lesion led to difficulties in determining those due to amputation of the flocculus from those arising from section of the eighth nerve, it was found necessary to eliminate the former by experiments confined to section of the floccular peduncle. These, therefore, are considered first.

1. The *flocculus cerebelli* was amputated in two cases.

This was revealed by exposing the lateral lobe of the cerebellum and gently

pulling it aside, when the pedunculus flocculi becomes clearly exposed to view. By aid of a sharp cutting hook, inserted upon the ventral side of the peduncle between it and the eighth nerve, the flocculus is readily severed from the cerebellum.

The symptoms following this operation are slight and transient. With the exception of a slightly unsteady gait and a tendency to fall on sudden movements, no marked symptoms of a cerebellar nature were observed.

2. In two cases the *eighth nerve was divided distal to the accessory auditory ganglion.*

The nerve was exposed in the same way as the flocculus cerebelli.

3. In two other experiments the *eighth nerve was divided proximally to and including the accessory auditory ganglion.*

In both instances this was done upon the left side. The symptoms following both these operations were similar, and may thus be briefly stated :—

The immediate and most obvious effect of severing the eighth nerve was to cause marked disturbances of equilibrium. The animals rolled many times in succession to the left, *i.e.*, towards the side of lesion. Apparently with the object of counteracting such rolling or the vertigo which gave rise to it, the monkeys lay on the belly with the limbs on the side of lesion abducted or extended, and those on the opposite side flexed by the side. Similar symptoms had been previously observed in cases in which the restiform body or inferior cerebellar peduncle had been divided (15, p. 749). The head was retracted and bent to the left side, while the chin was deflected and pointed to the right shoulder. The knee-jerks were equal and readily obtained on both sides. In the course of time, the profound disturbances of equilibrium subsided, so that the animals were able to move about, but in a sprawling and unsteady fashion.

As regards the sense of hearing in those cases, it was impossible to make out anything definite. For a time after the operation, the reflex from the right ear on jingling keys was in abeyance, but this was not always a constant phenomenon.

In two of the cases in which this operation was performed, the facial nerve lying subjacent to the eighth was also divided.

4. *Unilateral destruction (left-sided) of the posterior corpus quadrigeminum.*

This operation was performed by removing the occipital lobe, dividing the tentorium, and retracting the anterior margin of the vermis cerebelli, until the posterior quadrigeminal bodies were fully exposed. The galvano-caustic knife was then used to destroy the tubercle on the left side.

Immediately after the operation, there was noted conjugate deviation of both eyes to the left with contracted pupils. On the following day the monkey was able to move about without any evidence of palsy ; the eyes moved normally, and the pupils

were equal. Tested more especially as regards cutaneous sensation, this was found to be unaffected, the monkey being responsive equally on both sides to all the usual tests.

There was slight unsteadiness of gait, and a sprawling or awkward action of the limbs, more especially upon the left side.

Nothing definite could be made out as regards hearing.

For a few days after the operation, a right-sided hemianopsia was detected due to removal of the occipital lobe, but this passed off.

5. In two cases the *internal geniculate body* was destroyed, but, as this was associated with marked impairment of cutaneous sensibility on the opposite side of the body, from coexistent lesion of the subjacent tegmentum cruris, the description of the symptoms is reserved for consideration with the result of section of the other sensory tracts (Series D).

The internal geniculate body was exposed by the same procedure as that for destroying the posterior quadrigeminal tubercle, with the difference that, instead of retracting the vermis cerebelli, the posterior end of the cerebral hemisphere after removal of the occipital lobe was raised; by this means this ganglion was seen lying upon the outer surface of the tegmentum cruris, and was readily destroyed by the galvano-caustic knife.

6. *Unilateral destruction of the superior temporal gyrus.*

In neither of these cases was there any obvious evidence either of anæsthesia or motor paralysis.

As regards the sense of hearing, it was impossible to state whether the animals heard sounds less well on one side than on the other. In neither was the evidence from the usual tests of a constant nature.

DEGENERATIONS CONSEQUENT ON LESIONS OF THE AUDITORY SYSTEM.

(a) *Degeneration following Amputation of the Flocculus Cerebelli.*

This operation was followed by degeneration in the stump of the peduncle, which could be traced as a compact bundle as far as the angle formed by the roof and floor of the fourth ventricle. Here there was observed degeneration of those fibres which BRUCE (11) has described and figured as floccular fibres, occupying the position of the so-called "vestibular nucleus" of BECHTEREW (12).

At this point a scattering of floccular fibres occurs. Some were traceable into DEITERS' nucleus; others passed dorsally in topographical relation with the superior cerebellar peduncle towards the vermis cerebelli, where they terminated in the roof nuclei, an observation harmonising with those of BECHTEREW and STSCHERBACH (13)

in fœtuses; while the larger number were followed through the floor of the fourth ventricle in the grey matter of this region. It was doubtful where any crossed the raphé, nor was it certain that any entered directly the nucleus of the sixth nerve, as BRUCE has stated. These degenerations were confined to the level of the floccular peduncle, for no degeneration was observed to pass either upwards or downwards in the central nervous axis. The direct connexions of the flocculus therefore seem to be of a purely local nature, viz., with DEITERS' nucleus, the vermis cerebelli, and the tegmentum pontis.

(b) *Degeneration following Section of Eighth Nerve distal to the Auditory Ganglion.*

Degeneration was limited to the expansion of the vestibular nerve in the medulla and pons, the degeneration of the cochlear portion being arrested at the accessory auditory ganglion.

The vestibular degenerations were traced into the postero-lateral region of the medulla. Many of the fibres terminated in DEITERS' nucleus. A number of fibres, however, were traced beyond this nucleus towards the outer angle of the fourth ventricle, where they mixed with the floccular fibres already described. Numerous single degenerated arcuate fibres were also observed to pass from the neighbourhood of DEITERS' nucleus into the tegmentum, some of which terminated on the same side, while others crossed the raphé. No degenerated vestibular root fibres could be traced directly into the cerebellum, although some were seen in the superior cerebellar peduncle. Degenerated fibres were also seen to pass from DEITERS' nucleus towards the sixth nerve nucleus on the side of lesion; while an extensive amount of fine diffuse degeneration was observed in the grey matter of the floor of the fourth ventricle, the outer part of which forms the internal auditory nucleus.

From this it is evident that the vestibular root has an extensive connexion with the nucleus of DEITERS and the tegmentum; while there is also a probable direct connexion with the nucleus of the sixth nerve.

(c) *Degeneration following Lesion of the Nerve internal to and including the Accessory Auditory Ganglion.*

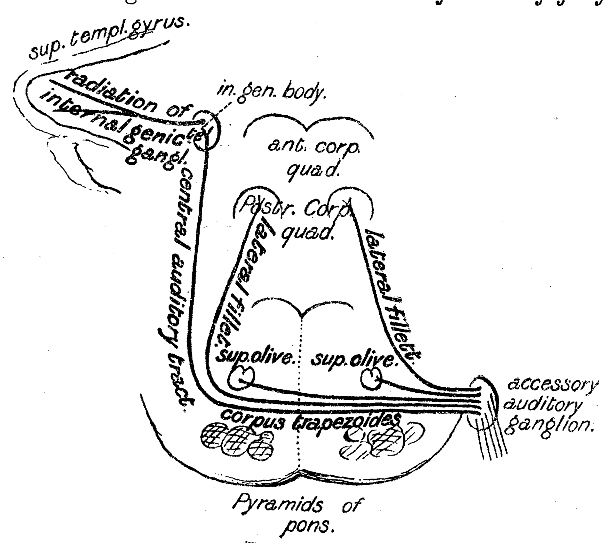
As a result of this lesion, the fibres of the trapezoid body were extensively degenerated. On the side of lesion, the degenerations formed a compact strand chiefly confined to the ventral aspect of this structure, but, on crossing the raphé, they spread out in a fan shape (Plate 2, fig. 1). A few fibres strayed from the main body, on the one hand into the pyramids, and on the other into the more ventral parts of the tegmentum. In intimate association with the degeneration of the corpus trapezoides, there was also degeneration of the superior olivary bodies. These exhibited degeneration on both sides, after a unilateral lesion, this being chiefly

limited to the inner of the two halves into which they are normally divided. In that on the side of lesion, the outer half also showed some degenerative change. The degeneration of the transverse trapezoid fibres appeared to stop ventral to the superior olive, this being the locality in which they turn at a right angle to pass up into the lateral fillet. A few fibres, however, passed on to the opposite accessory auditory ganglion, being probably commissural between these two structures. Degeneration was also traced both above and below the level of the lesion in the posterior longitudinal bundles, rather more extensively on the same side.

In sections made just above the level of the trapezoid body and behind the posterior quadrigeminal tubercles, the lateral fillet on both sides was found degenerated, but the alteration was more marked on the side opposite the lesion than in

Schema 2.

Scheme showing connexions of the accessory auditory *ganglion*.



The thick lines indicate degeneration.

that on the same side. It is noteworthy that the degeneration here was less extensive than in sections lower down, from the fact that many of the trapezoid fibres terminate in the superior olivary bodies, and others in the nucleus of the lateral fillet. Some of the fibres of the lateral fillet on the side opposite the lesion pass into the posterior quadrigeminal body, while all those on the side of lesion end in the corresponding tubercle.

In sections through the anterior quadrigeminal region, the degeneration on the side opposite the lesion occupied a definite position in the outer portion of the tegmentum cruris, just mesial to the internal geniculate body and in the position of the mesial fillet, which has here passed outward from the ventral and mesial situation it occupies lower down. There was no degeneration on the same side as the lesion.

In this locality the degeneration, secondary to destruction of the auditory ganglion, is extensive and intermingled with numerous normal fibres of the tegment. That these degenerated fibres enter the internal geniculate body was assumed from the fact that no evidence of their presence was detected in sections made higher up. This assumption, however, received confirmation and amplification from the examination of a case in which the posterior quadrigeminal body and lateral fillet were unilaterally destroyed. In this case, which is described in the next section (d), the degeneration of the fibres arising in the accessory ganglion of the opposite side was well marked, and was traced in diminishing quantity from the corpus trapezoides to the internal geniculate body. This proves conclusively the existence of a direct strand of fibres between the accessory auditory ganglion and the opposite internal geniculate body. Hence we are unable to confirm the statement of EDINGER (14) that this segment of the auditory path is interrupted, first, in the superior olivary body and, secondly, in the nucleus of the lateral fillet. From the fact that the auditory tract diminishes in extent as it is traced upwards, it may be argued that many of its fibres terminate in the superior olivary bodies, the nucleus of the lateral fillet, and the posterior quadrigeminal tubercles, but that a considerable number pass to the internal geniculate body uninterrupted (*vide* Schema 2). No degeneration was observed in the so-called peduncle of the superior olive, which passes from this body to the nucleus of the sixth cranial nerve, a fact which indicates that there is no *direct* connexion between the auditory nerve and the centre for conjugate movement of the globes.

(d) *Degenerations following Unilateral Destruction of the Posterior Quadrigeminal Body and Lateral Fillet.*

Consequent on this operation there was found a degenerated strand of fibres in the external portion of the tegmentum cruris, mesial to the internal geniculate body, in the position assigned to the continuation of the central auditory tract. In these sections it was more clearly seen that many of the degenerated fibres turned into the internal geniculate body, the ventral part of which showed a scattered degeneration, and that others passed on directly into the ventral portions of the optic thalamus. But in these sections the degeneration was more extensive than in those examined after lesion of the accessory auditory ganglion. As the structures destroyed consisted of both the lateral fillet and the posterior quadrigeminal body, the degeneration was made up of auditory fibres contained in and in association with the lateral fillet, as well as fibres arising *de novo* in the posterior quadrigeminal tubercle. These latter fibres were traced cerebralwards into the subthalamic region and ventral portions of the optic thalamus. Their position in this region and their further continuation will be again referred to (p. 28).

Another important degeneration was traced after lesion of this ganglion in a down-

ward direction. This is the tract which we have elsewhere described and figured as the "lateral fillet tract." In the previous research (15, p. 742) the statement was made that this bundle of fibres degenerated downwards after a lesion of the lateral fillet, but the more recent observations recorded in this paper show that this tract largely originates in the posterior quadrigeminal tubercle. In sections taken a short distance below the lesion it is found lying just mesial to the main body of the lateral fillet. From this position it was traced downwards in the tegmentum to the level of the motor nucleus of the fifth nerve, where it lies between this nucleus and the superior olivary body and on the mesial side of the motor trigeminal root, whence it may be followed into the posterior part of the lateral medullary region and onwards into the lateral column of the spinal cord, as elsewhere detailed and figured (15, Plate 67).

The observations of BOYCE (16) upon the descending internuncial fibres of the mid and hind brain indicate the presence of a system of fibres in the lateral medullary region and lateral column of the spinal cord which degenerate downwards after section of the opposite crus cerebri, the crossing taking place through FOREL'S "fountain" decussation. That these fibres occupy in the position of our "lateral fillet tract" is apparent from a comparison of the figures, but that they do not all arise from the opposite crus cerebri is evident from the facts recorded in this and a previous paper, which show that many come from the posterior quadrigeminal body and the lateral fillet of the same side.

(e) *Unilateral Destruction of the Internal Geniculate Body.*

From an inspection of fig. 6, Plate 2, which represents the amount and extent of lesion in these cases, it will be seen that the mesial fillet was also destroyed, as it lies immediately subjacent to the internal geniculate ganglion in the tegmentum cruris.

Hence the degenerations which we have observed result from destruction both of the geniculate body and of the mesial fillet. The degenerations due to interruption of fillet fibres will be described later on (p. 30).

Following destruction of the internal geniculate body as such, a tract of degenerated fibres was traced into the superior temporal convolution. One case, viz., that in which the ventral part of the optic thalamus and regio sub-thalamica were also involved, showed an extensive degeneration passing into the first as well as into the other temporal gyri, a degeneration which was regarded as the temporal part of the great thalamo-cortical system of fibres. But in the second case, in which the optic thalamus and sub-thalamic region were intact, no such extensive degeneration was detected, but a number of long fibres undergoing degeneration were found in the white matter of the first temporal convolution only, and in the

tissue ventral to the lenticular nucleus. In the sections at our disposal none of these fibres appeared to pass through the lenticular ganglion.

There was no clear evidence from this case that the radiation of the internal geniculate body passed through the optic thalamus.

Until a few years ago, much obscurity lay over the central connexions and continuations of the eighth nerve. As all the known methods of neurological research have been recently brought to bear upon this subject, an extensive literature exists upon the connexions of this nerve. By aid of these various methods of investigation, fairly harmonious results have been obtained; but it is difficult to distinguish the *direct* from the *indirect* connexions which the two divisions of this nerve form.

The general conclusion obtained from a study of the observations of KÖLLIKER (17), BECHTEREW (12), HELD (18), and BRUCE (11) is to the effect that the *vestibular nerve* ends mainly in DEITERS' nucleus; but that its other direct terminations are in the so-called "BECHTEREW'S nucleus," which may more properly be regarded as the dorsal continuation of DEITERS' nucleus (BRUCE), and in the ascending auditory root. The composition of the so-called "ascending auditory root" is a point on which some difference of opinion exists. It consists of fasciculi of nerve fibres scattered amongst grey matter containing large multipolar nerve cells. According to BRUCE, its lower end terminates in the nucleus of the funiculus cuneatus. We have been unable to detect any degeneration in this root after section of the eighth nerve, so that there is probably no direct passage of fibres from the nerve into the "ascending" root. It is more probable that it forms an internuncial connexion between the nucleus of DEITERS, which is a very extensive structure, and the cuneate nucleus.

These primary nuclei have numerous indirect strands of connexion :—

a. With the roof nuclei of the cerebellum by a tract which we have elsewhere shown degenerates after removal of the vermis cerebelli (15)—the so-called "direct sensory cerebellar tract" of EDINGER;

b. With the nucleus of the sixth cranial nerve;

c. With the tegmentum pontis;

d. With the lateral bulbar region and the anterior column of the spinal cord, by means of a tract which we elsewhere found degenerates after lesion of DEITERS' nucleus (15);

According to BRUCE, also with the inferior olivary body (19).

The central continuations of the fibres of the *cochlear* nerve, arising in the accessory auditory ganglion or end-nucleus of this nerve (KÖLLIKER), are by way of the corpus trapezoides and lateral fillet to the posterior quadrigeminal tubercle and internal geniculate body of the opposite side.

There can be no doubt, from the results of our experiments, that such a connexion exists between these structures, for destruction of the accessory auditory ganglion was followed by a tract of degeneration through the trapezoid body, with which the superior olives stand in close relation, to the lateral fillet of the opposite side. Our experiments confirm the view enunciated by FLECHSIG (20) and BAGINSKY (21) that the connexion between the eighth nerve and the posterior corpora quadrigemina is by way of the corpus trapezoides and lateral fillet.* (Schema 2.)

After destruction of the labyrinth in rabbits BUMM (23) and BAGINSKY found disappearance of the fibres of the opposite lateral fillet and some degree of atrophy of the posterior quadrigeminal tubercle and internal geniculate body; and VON MONAKOW (*op. cit.*), after destruction of the temporal lobe in young rabbits, observed atrophy of the corpus geniculatum internum of the same side.

The observations, from the standpoint of degeneration and atrophy, are confirmed by the anatomical researches of KÖLLIKER (17) and HELD (18), working by the method of GOLGI. These point to the existence of cells in the accessory auditory ganglion which emit as axis-cylinder processes the fibres of the trapezoid body, some of which terminate in the superior olives, others merely giving off collaterals to them, the remainder passing on through the lateral fillet to the opposite posterior corpus quadrigeminum.

We cannot state precisely to what extent the lateral fillet is affected by degeneration as a result of lesion of the accessory auditory ganglion. That the fibres of this structure mainly end in the posterior quadrigeminal body is obvious from the investigations of KÖLLIKER; but our sections show that a not inconsiderable number of fibres may be traced beyond the posterior quadrigeminal region to the internal geniculate body. Hence the fibres of the lateral fillet itself may form a connexion between the superior olive and the corresponding posterior quadrigeminal body, and indirectly with the accessory auditory ganglion; while the fibres of the central auditory tract either help to form, or lie in association with, the lateral fillet.

A continuation of some of the fibres of the lateral fillet beyond the posterior quadrigeminal body has been described both by KÖLLIKER and HELD, but the latter's statement that fibres can be traced through the quadrigeminal region, the regio-subthalamica, and the internal capsule to the cortex of the temporal lobe, so as to form a "direct cortical auditory tract," has not been confirmed by KÖLLIKER (vol. 2, p. 396).

The probable existence of a strand of fibres passing from the internal geniculate body to the superior temporal convolution has been stated by numerous observers; while the fact that it medullates at a definite period of intra-uterine life has been recently established by FLECHSIG (8B). This radiation of the internal geniculate body

* VON MONAKOW'S (22) observation that section of the lateral fillet produced atrophy of the striæ acusticæ and of the tuberculum acusticum, without any alteration in the trapezoid body, does not militate against the observations here recorded.

ascends through the optic thalamus, and crosses the posterior part of the internal capsule and the putamen, to end in the superior temporal gyrus. This tract corresponds with the "direct cortical auditory tract" of HELD.

The results which we have obtained from the study of the degenerations by MARCHI's method point to the following conclusions :—

1. That the cochlear fibres end in the accessory auditory ganglion.

2. That in the auditory ganglion the trapezoid fibres arise, some of which pass through the lateral fillet of the same side, and some cross to the opposite side.

3. That the superior olivary bodies have a close and direct connexion with the fibres of the corpus trapezoides, degenerating when this structure is severed from the accessory auditory ganglion.

4. That the fibres of the lateral fillet coming from the auditory ganglion end in the posterior quadrigeminal body of the same and the opposite side, and others pass on to the internal geniculate body of the opposite side.

5. That of the fibres arising *de novo* in the posterior quadrigeminal body some pass upwards to the sub-thalamic region, and others pass downwards into the lateral column of the spinal cord.

6. That there is no evidence that fibres pass directly from the lateral fillet to the cortex of the temporal lobe, without interruption in the internal geniculate body.

(Some further facts on the connexions of the optic thalamus and the cerebral cortex are given in Section D.)

(f) *Destruction of the Superior Temporal Gyrus.*

When sections were made through the crura cerebri in the cases in which this operation had been performed, degeneration was observed in those fibres which occupied the outermost bundles of the pes. In frontal sections of the upper portion of the quadrigeminal region, this degeneration chiefly occupied definite fasciculi in the outer portion; on passing lower down it was confined to approximately the outer fifth or fourth. This degeneration was traced through the crus in this situation into the upper portion of the pons, where it gradually disappeared from view; but there was no clear evidence as to the destination of this bundle, although the probability is that it ends in relation with the nucleus pontis. Its cerebral division lies between the superior temporal gyrus, from which it arises, and the foot of the crus cerebri. No individual sections at our disposal showed the whole course of these fibres from their origin in the superior temporal gyrus to their entrance into the outer region of the pes cruris. But from a series of sections it was determined that they reached this position by crossing the retro-lenticular part of the internal capsule, ventral to the lenticular nucleus, in the position assigned to them by DÉJÉRINE (27) in man.

Of other degenerations following this lesion, there were observed—

a. A strand of degenerated fibres which passed into the outer limb of the forceps corporis callosi, and thence by way of the splenium to the opposite cerebral hemisphere, thus forming a commissure between opposite lobes.

b. A number of degenerated fibres passing round the base of the Sylvian fissure to enter the white matter of the angular gyrus.

c. A marked amount of degeneration in the white matter of the occipital lobe, lying between the optic radiations and the external occipital cortical grey matter:—the stratum proprium occipitale of SACHS.

b and *c* are probably associating fibres.

It was important to note the entire absence of degeneration in the posterior quadrigeminal bodies and the lateral fillet, which, as we have seen, degenerate after lesion of the accessory auditory ganglion.

In VON MONAKOW'S (22) experiments upon the superior temporal gyrus in young animals, it is stated that atrophy of the internal geniculate body and of part of the internal capsule was observed. These observations do not militate against our statement that no *degeneration* was found in them after a similar lesion in adult monkeys, but merely corroborate the existence of the afferent cortical tract already described as the central auditory path.

The presence of a descending or corticifugal tract in the outer portion of the pes cruris was originally described by BECHTEREW (24) and ROSSOLYMO (25), but it was for some time uncertain from which portion of the cerebral cortex it arose. ZACHER (26) found this tract degenerated after a cortical lesion involving the first temporal gyrus and the cuneus. The more recent investigations of DÉJÉRINE (27), however, place its origin in the cortex of the second and third temporal gyri. The existence of this tract has also been demonstrated by the myelination method of FLECHSIG (8A). Our observations show that a large number of fibres occupying the external portion of the pes cruris—the external pontine system of BECHTEREW—degenerate after a lesion limited to the first temporal convolution.

The most recent observations of FLECHSIG (8A) indicate that this tract does not wholly arise from the temporal lobe; but he does not state from which other part of the cortex they spring. There was no evidence, from our experiments, that this tract received fibres either from the occipital lobe or the angular gyrus, for removal of these structures was not followed by any degeneration in this locality. But it was observed in the two experiments in which the superior temporal gyrus was destroyed that the subsequent degeneration was more extensive in the case in which the cortical lesion was more widespread, viz., that in which the second temporal gyrus was largely involved (Plate 1, fig. 6). Hence it may be argued that the origin of this tract is not limited to the superior temporal convolution, but includes also the second convolution, as DÉJÉRINE has stated.

What the function of the tract may be is more difficult to determine. The

monkeys in which the superior temporal gyrus was destroyed presented no other obvious symptoms than those already described (p. 15). It would appear to be a temporo-pontine tract corresponding in its destination to the fronto-pontine tract, to which reference will later on be made, and to form the corticifugal bundle complementary to the great corticipetal system of auditory fibres which reaches the first temporal convolution.

The other degenerations following lesion of the temporal lobe indicate that there exists a commissural connexion between the temporal gyri of opposite sides by way of the forceps exterior and the corpus callosum; and that associating fibres join this region with the angular gyrus lying above it and the occipital lobe lying posteriorly.

From the preceding observations it would appear that in the cerebral segment of the auditory system, as in that of the visual, there exist two sets of fibres, one *corticipetal*, subserving audition proper; the other *corticifugal*, the function of which is undetermined.

Our observations by the degenerative method show that there is an interruption of the cochlear fibres in the auditory ganglion, and that the fibres from this structure terminate in the superior olivary bodies, the posterior quadrigeminal tubercles, and the internal geniculate body of the opposite side, from which a tract ascends to the superior temporal gyrus. There was also evidence that some of the fibres of the lateral fillet pass directly into the optic thalamus. From this it would appear that the auditory system is interrupted in the internal geniculate body and optic thalamus in a manner comparable to the breakage of the visual system in the external geniculate body and pulvinar. There was, on the other hand, no evidence that the posterior quadrigeminal bodies hold a position in the auditory system analogous to that of the anterior quadrigeminal bodies in the visual system, as there was no degenerative alteration in these structures after extirpation of the cortical auditory area.

SERIES C.

Other Afferent Cranial Nerves.

The other afferent cranial nerves which were the subject of experiment are the trigeminus and the glossopharyngeus.

(a) *Division of the Sensory Trigeminal Root between the Gasserian Ganglion and the Pons* (Exp. 20).

As the degenerations following this lesion have been elsewhere (15) fully detailed, it is considered necessary here only to recapitulate the chief facts. This operation was invariably followed by degeneration of the so-called "ascending" trigeminal root

in the pons and medulla oblongata, which was traced spinalwards as far as the tubercle of ROLANDO. This root progressively diminishes in size as it is traced distally by the passage of its fibres into the subjacent gelatinous substance. As no degeneration was observed to pass from this structure into the tegmentum, or into the posterior horn, it was evident that in this substance lay the end-nucleus of the sensory trigeminal fibres whose cells of origin are situated in the Gasserian ganglion. That the secondary neurons arising in the gelatinous substance cross the raphé, and are continued cerebralwards in the tegmentum pontis of the opposite side in association with the cutaneous sensory fibres of the body and limbs, was obvious from the fact of the experiments where section of the tegmentum cruris was followed by anæsthesia of the whole of the opposite side, including the face (Exps. 24 and 25).

The symptoms following section of the trigeminal nerve and of its ophthalmic branch have been elsewhere detailed (28 and 29).

The general statement may here be made, that the common views as to the causation of neuro-paralytic ophthalmia were not confirmed. Of the eighteen experiments in which anæsthesia of the cornea was the prominent symptom, only two showed evidence of destructive corneal change and panophthalmitis; and in both of these there was evidence of septic irritation. The general conclusion drawn from a study of these experiments was that there existed no evidence of trophic influence exerted by the Gasserian ganglion upon the cornea, and that, provided inflammatory irritation is prevented, the ophthalmic branch may be safely divided, or the Gasserian ganglion removed without fear of the disorganisation of the eye. Hence the so-called neuro-paralytic phenomena associated with lesion of the trigeminus are evidence of irritation of the nerve, and not of cessation of function.

(b) *Division of the Glossopharyngeal Nerve Roots* (Exp. 21).

This operation was followed by degeneration of—

a. The intra-medullary root fibres passing inwards from the periphery;
b. Many of the fibres of the so-called "solitary bundle" or ascending glossopharyngeal root;
c. Some of the fibres in the grey matter of the floor of the fourth ventricle, in the position of the posterior vago-glossopharyngeal nucleus.

We were enabled by this degeneration to trace the ascending vago-glossopharyngeal root distally as far as the level of the pyramidal decussation in the dorsal part of the reticular formation, and just outside the grey matter which encircles the central canal at this level.

As in the case of the ascending trigeminal root, with which the ascending vago-glossopharyngeal root is homologous, a progressive diminution in size occurs from the passage of its fibres into the gelatinous substance which forms the end-nucleus of

its fibres (Kölliker). There was no evidence from degeneration as to the course of the fibres arising in the end-nucleus. It is, however, probable, reasoning by analogy, that they cross the raphé and are continued cerebralwards in the tegment of the medulla, pons, and crus cerebri.

In dealing with the cerebral continuation of these two nerves, there is no direct evidence from degeneration of the passage of their secondary neurons across the raphé. As regards the crossing of the sensory trigeminal fibres, the clinical facts, however, are sufficiently explicit, for, in the cases in which the tegmentum cruris was divided, anæsthesia of the face coincided with that of the body and limbs on the opposite side. It would therefore appear that the cerebral continuations of the afferent cranial nerves (with the exception of the auditory) lie in the tegment of the hind brain, in close relation with the sensory tracts of the body and limbs.

Bechterew (12) places the central continuation of the vagus and trigeminal nerves amongst the so-called "scattered fillet fibres," which lie internal to the chief fillet. According to him, their termination is in the parietal region of the cortex cerebri. Edinger (31), on the other hand, working with the myelination method, places the central tract of the trigeminal nerve in the dorsal part of the tegment, lateral and rather ventral to the posterior longitudinal bundles. The existence of this tract, which has been also found in rabbits by Wallenberg (30) to degenerate after section of the fibres as they leave the trigeminal end-nucleus, is indicated in man by the presence of numerous fibres in a similar position, although there is no evidence that they belong to the trigeminal system. In rabbits, this system ends in the ventral nucleus of the optic thalamus.

(Further facts on the sensory path in the pons are given in Series D, p. 32.)

SERIES D.

The Cutaneous Sensory and other Corticipetal Systems.

For the investigation of this subject the sensory path was divided as high up in the hind brain as was possible and compatible with survival, the operation being naturally a severe one.

The experiments were—

1. Hemisection of the tegmentum pontis immediately behind the posterior quadrigeminal body (Exps. 22, 23).
2. Hemisection of the tegmentum cruris at the level of the internal geniculate ganglion (Exps. 24, 25).

1. *Hemisection of the Tegmentum Pontis.*

This is a serious operation, and in several instances the animals succumbed. In two, however, life was sufficiently prolonged to permit of a satisfactory study of the symptoms.

The floor of the fourth ventricle was exposed by the same method as is required for the posterior quadrigeminal body. A knife, carefully guarded as to the depth to which it should be passed, was inserted perpendicularly in the middle line and carried transversely outwards.

In both cases the operation was performed upon the left side, and the symptoms were similar.

All down the right side of the body, with the doubtful exception of the face in one instance, there was complete anæsthesia and analgesia to all the usual tests. On the side of the lesion, the response to cutaneous irritation was so active as to suggest hyperæsthesia. There was absolutely no motor palsy of the limbs.

In one of these cases some interesting ocular phenomena were observed, and, although not bearing directly upon the subject under discussion, may be mentioned here. During the six days of life after the operation there was *persistent conjugate deviation of both eyes to the right*, with inability to move them to the left. During the same period there was also weakness, not amounting to paralysis, *of the orbicularis palpebrarum* on the side of lesion.

These phenomena may be ascribed to division of the posterior longitudinal bundle, which was revealed at the post-mortem examination. The conjugate deviation indicates that the centrifugal path from the cerebral cortex to the opposite sixth nerve nucleus decussates in the neighbourhood of the quadrigeminal bodies, and passes downwards in the tegmentum pontis; and it also points to the fact that the fibres from the sixth to the opposite third nucleus decussate at once on leaving the abducens nucleus and pass up by the opposite tegment, probably in the posterior longitudinal bundle; for if this were not so, there would have been deviation to the left of the eye on the side of lesion without a coexistent conjugate deviation of the right eye.

The weakness of the orbicularis palpebrarum on the side of lesion lends support to the view that some of its fibres of innervation arise in the third nerve nucleus and pass downwards in the posterior longitudinal body, which was divided in our experiment.

Subsequent microscopic examination of the pons Varolii in both these cases showed that the tegmentum was divided on the left side, as well as the mesial fillet wholly or partially. But, as the animals did not live sufficiently long, we are unable to give an account of secondary degenerations.

The relations of the tegmentum and of the mesial fillet to cutaneous sensation will be discussed later on (p. 31).

2. *Hemisection of the Tegmentum Cruris.*

The steps of this operation are similar to those for destroying the internal geniculate body. In both cases in which this latter operation was performed the tegmentum cruris was destroyed.

It was impossible in either case to make out anything definite as regards hearing; but the animals were temporarily hemiopic to the right from the fact that the occipital lobe was removed.

Although the limbs on the side opposite the lesion (right) were freely moved during struggling, in climbing their action was awkward; moreover, they were flaccid immediately after the operation, and offered no resistance to passive movement. Further testing showed that there was complete anæsthesia and analgesia on the side opposite the lesion (face, ear, arm, body, and leg). There was no attempt at localisation of the clip when applied to this side. On the side of lesion the response to all forms of cutaneous irritation was active.

This condition remained in one of the cases until death, one month after the operation, and in this experiment the destruction of the tegmentum cruris was complete and extended into the sub-thalamic region and optic thalamus.

In the other case, although anæsthesia persisted, the analgesia diminished.

Degenerations following Lesions of the Tegmentum and its Ganglia.

In describing the degenerations included under this heading, we enter upon a subject of great complexity, for it is possible that amongst the tracts ascending to the cortex there are some subserving conscious sensation, while it is probable that there exist other systems of fibres conducting impressions of a merely afferent nature. Amongst this latter class should probably be placed the fibres of the posterior columns of the spinal cord continued by the mesial fillet, efferent cerebellar fibres conveyed by the superior cerebellar peduncle, and ascending fibres from the posterior quadrigeminal bodies.

The experiments bearing on this subject were—

a. Unilateral destruction of the posterior quadrigeminal body, including the lateral fillet and adjacent portion of the tegmentum pontis (Exp. 13).

b. Destruction of the internal geniculate body, including the adjacent portion of the tegmentum cruris (Exp. 14).

c. Destruction of the pulvinar and adjacent portions of the optic thalamus and tegmentum (Exp. 15).

a. *Destruction of the posterior quadrigeminal body,* including the adjacent portion of the lateral fillet, tegmentum pontis, and superior cerebellar peduncle.

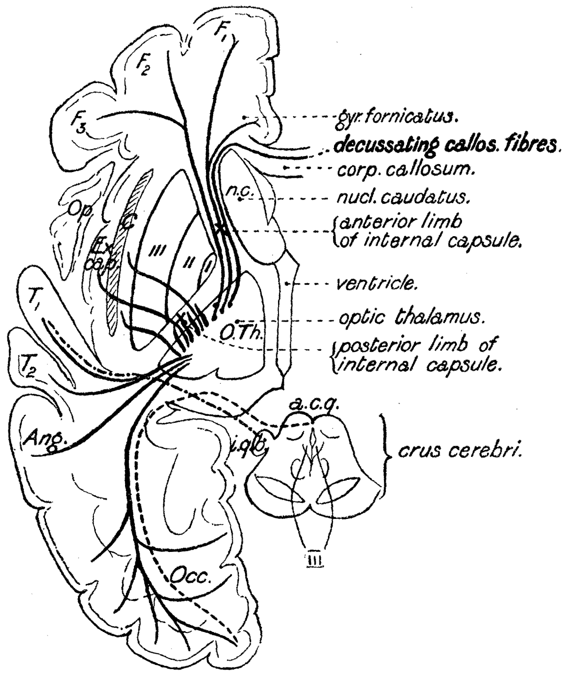
Leaving out of consideration the degenerations descending from this lesion, which have been already described (p. 18), we shall confine our attention to those observed in the examination of sections through the regions above the seat of the operation.

At the level of the anterior quadrigeminal body an extensive area of degeneration was observed in the outer portion of the tegmentum cruris, occupying the position of

the central auditory tract and mesial fillet. The degeneration was much more extensive than that following destruction of the accessory auditory ganglion alone, which has been already described (p. 18). The question then arises, "Whence do these fibres come?" and the probable answer is that they are fibres arising *de novo* in the posterior quadrigeminal body and passing in a corticipetal direction. There seemed to be no doubt, from sections made through the internal geniculate body, that many fibres from the lateral fillet and posterior quadrigeminal body end in this ganglion, while others were traced directly into the regio sub-thalamica and ventral portions of the optic thalamus.

Schema 3.

Schematic horizontal section of the left cerebral hemisphere, showing the *thalamic corticipetal* fibres.



Dotted thick line = radiation of internal geniculate body.
Dotted thin line = occipital corticifugal tract to the anterior quadrigeminal region.

The examination of frontal sections at higher levels, viz., through the sub-thalamic region, the optic thalamus, and the lenticular portion of the internal capsule, showed degeneration in the dorsal portion of the regio sub-thalamica in the position in which we had previously found the mesial fillet and superior cerebellar peduncle, and a well-marked, though scattered, degeneration in the ventral and lateral portions of the optic thalamus, anterior to the pulvinar. Both these degenerations were traced beyond the optic thalamus into the posterior limb of the internal capsule, through which chiefly, and to a lesser extent through the lenticular nucleus and external capsule, they were followed to the cerebral cortex. The particular

convolutions to which they were traced were those lying above the fissure of SYLVIUS, and more especially the superior parietal lobule and the marginal convolution on the mesial aspect.

Continuing the series of frontal sections forward through the cerebrum, this large corticipetal strand was found also passing up the anterior limb of the internal capsule, but was here not so extensive. The white matter of the three frontal convolutions and of the Rolandic area showed a considerable number of degenerated fibres right up to the under-surface of the grey cortex. The condition of the falciform lobe was also noted. In the sections at our disposal no degeneration was observed in the gyrus hippocampi; on the other hand, an obvious degeneration of the fibres of the gyrus fornicatus and cingulum was seen, more pronounced in the posterior regions of the cerebrum than in the anterior.

A considerable number of the degenerated fibres, which passed up the internal capsule, crossed to the opposite hemisphere by way of the corpus callosum.

In addition to this degeneration, another was observed, but smaller in amount, in the position of the red nucleus of the tegmentum cruris, occupying the position of the uncrossed fibres of the superior cerebellar peduncle, which was injured by the lesion. These fibres were also traced into the sub-thalamic region.

b. The degenerations following *lesion of the internal geniculate body* have been already described on p. 19. Those which were due to the coexistent interruption of the fibres of the subjacent mesial fillet are described in the following paragraph.

c. *Destruction of the pulvinar thalami and adjacent portions of the optic thalamus and tegmentum.*

The degenerations following this lesion were studied in a series of frontal sections through the cerebral hemisphere and basal ganglia. The operation necessitated removal of the occipital lobe, but the occipital degenerations following lesion of the pulvinar have been already described in a case in which this ganglion was destroyed from above, after division of the corpus callosum, without injury to the occipital region (p. 10).

A great system of corticipetal fibres was traced from the optic thalamus through the centrum ovale to the cortex cerebri. The distribution of this degeneration was as follows:—

(1) A large and well-defined mass of fibres passing to the angular gyrus (see also p. 9).

(2) Another and equally well-marked series of fibres ascending to the superior temporal convolution, these fibres reaching this area partly through the lenticular nucleus and partly beneath it. A slighter and less well-defined degeneration was also traced into the other temporal gyri.

(3) Degeneration was also observed in the white matter of the gyrus fornicatus and of the cingulum and gyrus hippocampi.

(4) A large strand of degenerated fibres passed into the superior parietal lobule, the cortex of the Rolandic area, and the marginal gyrus.

(5) An examination of sections from the frontal lobe at the level of the anterior end of the corpus striatum showed a small amount of degeneration passing into the three frontal gyri. This was not so extensive as that passing into the other portions of the cortex, and there was no degeneration of the frontal portion of the gyrus fornicatus and cingulum.

The route by which this system of degenerated fibres passed from the thalamus to the several cortical areas above mentioned was chiefly by way of both limbs of the internal capsule, mingling with the pyramidal and other fibres in this structure, to a lesser extent through the lenticular nucleus and putamen, and thence by the external capsule.

Many of the fibres which passed up the internal capsule crossed to the opposite hemisphere by way of the corpus callosum.

This observation supports the view of HAMILTON (40), that the corpus callosum is not only a commissure uniting similar regions of opposite hemispheres, but also "a decussation of certain cortical fibres, which do not decussate lower down."

This tract of fibres, to which HAMILTON has given the name of "crossed callosal tract," degenerates, according to our observations, in a corticipetal direction, and passes from the optic thalamus to the cortex of the opposite cerebral hemisphere.

A critical examination of this series of experiments leads to some important conclusions.

First, in two of the cases, viz., those in which there was a destructive lesion of the tegmentum cruris, the clinical phenomena were permanent anæsthesia and analgesia of the whole of the opposite side of the body, facts which indicate that in the region lying external to the red nucleus, and between the anterior quadrigeminal body and the substantia nigra, is situated the sensory tract of the tegmentum cruris (Plate 2, fig. 6). In this region lie the mesial fillet, the central auditory tract, and ascending fibres of the posterior quadrigeminal body. This last structure may be destroyed as in Exp. 13, the central auditory tract may be degenerated as in Exps. 11 and 12, and also the mesial fillet (15, *op. cit.*), without any obvious impairment of cutaneous sensibility. The only remaining tissue in this region is the continuation of the short fibre systems or reticular formation of the tegmentum of the pons and medulla. By a process of exclusion therefore we conclude that the path of cutaneous sensation is in this formation.

We have elsewhere concluded, from other experiments (29B), that at the junction of the spinal cord and medulla the path of cutaneous sensibility is probably situated

in the gelatinous substance of ROLANDO. As this structure is not traceable higher than the so-called sensory nucleus of the trigeminal nerve, it might, *à priori*, be assumed that it is continued upwards in the short fibre systems of the tegmentum of the pons and crus. This is, in reality, borne out by our experimental results.

For it is seen that in both the cases in which this portion of the tegmentum cruris was destroyed anæsthesia and analgesia resulted.

The position occupied by the sensory path in the tegment of the pons is a question on which there is much diversity of opinion. NOTHNAGEL holds that it is situated laterally and near the floor of the fourth ventricle; but STARR (32), from his investigation of recorded clinical cases, has placed it in the mesial fillet. MOELI and MARINESCO (33) from similar data arrived at the conclusion that the paths of cutaneous sensibility lie either in the mesial fillet alone, or in this together with the neighbouring portion of the reticular formation. Though in our experiments, in which anæsthesia and analgesia were observed after section of the tegmentum pontis, the mesial fillet was also divided, yet, inasmuch as we have found that the fillet may be entirely sclerosed without impairment of sensation, we are led to the conclusion that the sensory path is in the reticular formation alone.

Secondly, the long fibre systems of the tegment, viz., the mesial fillet, the superior cerebellar peduncle, and the posterior quadrigeminal ascending fibres, pass directly into the optic thalamus, and more especially into its ventral and external portions. In a previous research upon this subject we were unable to follow any direct cortical continuation of these systems. But the method of MARCHI has enabled us to trace degenerated fibres beyond the optic thalamus. The observations recorded in this paper harmonise with those of FLECHSIG and HÖSEL (34) as to a direct cortical prolongation of the mesial fillet—the so-called "cortical fillet" of these observers. The superior cerebellar peduncle may also ascend to the cortex, as EDINGER (31B) and FLECHSIG hold; but a large number of fibres of both systems undoubtedly end in the optic thalamus.

We have, however, been unable to differentiate, amongst the great mass of corticipetal fibres leaving the optic thalamus, those which belong to the mesial fillet and superior cerebellar systems from those which form the path of cutaneous sensibility.

The observations of FLECHSIG and HÖSEL (34) place the cortical termination of the fillet, and probably also of the superior cerebellar peduncle, in the Rolandic area, and chiefly the posterior central convolution, for in a case of old-standing softening of this area secondary atrophy was observed in the superior peduncle, the mesial fillet, the reticular formation, and the lateral region of the optic thalamus. The experiments of MONAKOW (35) upon the post-central area are corroborative of the above, for he found that extirpation of this area in young animals was followed by secondary atrophy in the fillet and in the nuclei of the posterior columns of the spinal cord.

Thirdly, our investigations show that a great system of corticipetal fibres passes out of the ventral and lateral parts of the optic thalamus to terminate in the grey matter of the cerebral convolutions on the mesial aspect, and on the convexity from the frontal to the occipital regions.

The course taken by these fibres is chiefly through both limbs of the internal capsule, and to a lesser degree through the lenticular nucleus and external capsule.

It is difficult in a purely histological investigation to distinguish amongst degenerated fibres those which are sensory proper from those which may be merely centripetal in character. For it may not be assumed, without further inquiry, that all the fibres which degenerate in a corticipetal direction are necessarily the paths of sensation proper.

According to the recent work of FLECHSIG (8A) upon the myelination of the fibres of the centrum ovale in the human fœtus, it is stated that the thalamo-cortical system may be divided into three sub-systems of fibres, viz.:—

(1) Fibres passing from the optic thalamus to the cortex of the Rolandic area which medullate at the ninth month of intra-uterine life. These ascend towards the cortex, partly by the posterior limb of the internal capsule, and partly through the lenticular nucleus and external capsule; and form the direct continuation of the mesial or so-called "cortical fillet"—"first sensory system."

(2) Fibres passing to the falciform lobe—gyrus hippocampi, cingulum, and gyrus fornicatus—which medullate during the first month of extra-uterine life—"second sensory system."

(3) Fibres, occupying the middle part of the internal capsule, which medullate from one up to several months after birth. These pass by way of the anterior limb of the internal capsule to the frontal convolutions as far as the anterior pole, and also to the gyrus fornicatus—"third sensory system."

It is only possible to determine the function of these several corticipetal systems by considering them in relation with the results of experiment.

a. We have elsewhere shown that the fillet may be entirely degenerated, and the nuclei from which it takes origin destroyed (clavate and cuneate nuclei), without any obvious impairment of cutaneous sensibility, an observation confirmed by MOTT (36). The only noticeable effect in our experiments was a temporary awkwardness in the movement of the limbs and a sprawling gait.

It would therefore appear that this system, which is the corticipetal continuation of the posterior columns of the spinal cord, subserves the conduction of afferent impressions, other than those of cutaneous sensation proper, necessary for the due co-ordination and regulation of movements.

b. No previous attention has been given to FLECHSIG'S "second sensory system." This observer is the first to describe a definite system of fibres, medullating at an early

period of extra-uterine life, which passes from the optic thalamus to the gyrus fornicatus. Destruction of this convolution experimentally in monkeys, according to the experiments of FERRIER (1), HORSLEY and SCHÄFER (41), is followed by anæsthesia and analgesia on the opposite side of the body. In two of our experiments (Nos. 13 and 15) we traced a degeneration into the white matter of this gyrus and the cingulum. In the one of these (Exp. 15), in which the pulvinar and adjacent part of the tegmentum and optic thalamus were destroyed, anæsthesia and analgesia of the opposite side existed as long as the animal lived ; while in the other (Exp. 13), in which the posterior quadrigeminal body, lateral fillet, and adjacent portion of the tegment were destroyed, no such symptoms occurred. Hence, though the sensory tracts proper end in the gyrus fornicatus, yet it would appear that this convolution is also the termination of tracts of a purely corticipetal character, a view which harmonises with FLECHSIG's observation that some of the fibres belonging to his "third sensory system," viz., those ending chiefly in the frontal lobe, also pass into the gyrus fornicatus.

c. FLECHSIG's "third sensory system" ascends from the optic thalamus by way of the anterior limb of the internal capsule to terminate in the convolutions of the frontal lobe.

FLECHSIG (8B) has pointed out that, although the optic thalamus is connected with the several regions of the cerebral cortex to almost an equal extent, this is not so with the frontal pole, where the thalamic fibres are evidently scanty, a fact which we have been able to confirm from our observations. This is the corticipetal system complementary to the descending tract of fibres which degenerates after removal of the frontal lobe, to be described in the next section. (Series E.)

With the exception of FLECHSIG's "second sensory system," the fibres which we have described as degenerating after lesion of the optic thalamus to the frontal, Rolandic, parietal, angular, and temporal regions of the cortex, form the "corona radiata thalami" of anatomists. It has been generally assumed that these fibres conduct in an efferent or corticifugal direction. The results of our experiments show that this is not the case. They appear to be the cerebral continuation of the tracts direct and indirect which enter the thalamus from below, viz., the mesial fillet, the superior cerebellar peduncle, posterior quadrigeminal fibres, the short fibre systems of the tegment, and partly also the lateral fillet containing the central auditory tract. The "corona radiata thalami" is, therefore, corticipetal in function.

Another structure to which reference has not been previously made, viz., the "central tegmental tract" of BECHTEREW, which passes from the inferior olivary body upwards into the tegment of the crus cerebri, is stated to have its cerebral continuation in the ansa lenticularis (OBERSTEINER).

Although, in one case (Exp. 13), this "central tegmental tract" was destroyed, and degeneration of its fibres traced to the inferior olivary body, there was no evidence from degeneration of a cerebral continuation.

The general conclusion which may be drawn from these observations is, that the

Rolandic area, like the visual and auditory centres, has a double relation with the periphery. On the one hand, there exists a *corticifugal* system, in this case the pyramidal tract; on the other hand, a *corticipetal* system, passing to the central convolutions and marginal gyrus.

Whether a tract efferent from the gyrus fornicatus exists complementary to the afferent system of this convolution is at present uncertain. FLECHSIG's observations by the myelination method failed to determine the existence of any such system. FRANCE (37), however, has described descending degeneration in the pyramids and crossed pyramidal tract of the spinal cord after destruction of the gyrus fornicatus. As in the performance of this experiment it is difficult to avoid injuring the marginal convolution, it is not improbable that this descending degeneration, as described by him, is in reality due to lesion of motor centres or tracts.

SERIES E.

THE FRONTAL AND PRE-FRONTAL SYSTEMS.

We have in the previous section described the afferent or corticipetal fibres of the frontal system. The operations about to be described were undertaken with a view to determine, by the degenerative method, the connexion of the tract of fibres which is stated to arise in the pre-frontal lobe and pass downwards as far as the pons Varolii.

The experiments were—

1. Extirpation of the pre-frontal lobe (Exps. 26, 27, 28).
2. Extirpation of the frontal lobe anterior to the pre-central sulcus, and its prolongation upwards to the superior longitudinal fissure (Exps. 29, 30).

1. The posterior boundary of the pre-frontal lobe was determined in each case by electrical stimulation, and the non-excitable portion of this lobe only removed.

Our recent researches have not added anything to the facts already known in connexion with the functions of this area.

2. In a case in which *both frontal lobes were removed in front of the pre-central sulcus,* certain phenomena were observed which had not been previously noted in experiments upon this region.

The frontal lobes were removed in two operations, the first consisting of extirpation of the left lobe. On the cut surface of the brain were seen the nucleus caudatus and the anterior part of the internal capsule, but the lateral ventricle was itself not opened.

The operation was followed by deviation of both eyes to the left, and there was slight paresis of the right arm and leg. For five days the monkey remained in a dull, sleepy condition, out of which it could be temporarily roused by stimulation, but into which it at once relapsed. At the end of this time it brightened up, and

on testing the vision it was found to be hemiopic to the right side. This was repeatedly observed and confirmed on subsequent examinations. Although there was no actual loss, there was distinct impairment of cutaneous sensibility on the right side. The right-sided hemiopia, which at first appeared complete, gradually lessened, and by the end of three weeks it was difficult to establish; while the only impairment of cutaneous sensibility was defective localisation of a small clip attached to the right limbs.

The right frontal lobe was then removed, but, as was found post-mortem, less extensively. There was no evidence of hemiopia after the second operation, or of impairment of cutaneous sensation. The characteristic mental condition, which has been described as consequent upon removal of the frontal lobes, was well seen in this instance. The second operation was followed by deviation of both eyes to the side of lesion, with inability to turn them to the opposite side, but this passed off in the course of a few days.

In another case the left frontal lobe was removed in front of the pre-central sulcus immediately anterior to the "leg area" as defined by the faradic current. The only symptom noted in this case was temporary deviation of both eyes and head to the side of lesion. There was no clear evidence of hemianopsia.

When the results of these experiments are taken in conjunction with those already described after removal of both frontal lobes and angular gyri (p. 5), it is seen that, apart from temporary inability to move the eyes conjugately to the opposite side, there is no permanent paralysis of the ocular movements. It would, therefore, appear as if other centres were sufficient to establish compensation when the so-called cortical areas of the head and eye movements have been removed.

The *temporary* hemianopsia and impairment of sensibility following extensive removal of the frontal lobe in one case deserves special attention. It is impossible, in view of previous observations on the visual centres, to believe that the centre of vision is also localised in the frontal lobe. The results should be considered in relation with those which we have recently obtained after extensive lesion of the Rolandic area. In three cases of extensive or complete destruction of the Rolandic area, we have observed, in addition to the motor palsy of the limbs, temporary hemianopsia and hemianæsthesia on the side opposite the lesion, without direct implication of the optic radiations or gyrus fornicatus as determined post-mortem.

The temporary presence of these symptoms, which HITZIG (39) has also observed, may therefore be explained by a dynamic influence exerted by the magnitude of the lesion on the sensory centres or tracts which were not organically injured.

This explanation receives support from the fact that in smaller cerebral lesions—for example, after removal of the so-called "leg area" alone—no such symptoms occurred.

Degenerations following Removal of the Frontal and Pre-frontal Lobes.

1. Extirpation of the pre-frontal lobe.

A constant tract of degeneration followed this operation. It occupied in frontal sections of the hemisphere the most mesial and ventral part of the anterior limb of the internal capsule immediately above the anterior commissure. With the exception of a few bundles of fibres lying in the caudate nucleus, and which appear to have diverged from the pre-frontal tract, the corpus striatum showed no evidence of degeneration, neither was any found in the opposite internal capsule, nor in the genu of the corpus callosum.

In more posterior sections, the degeneration occupied the same relative position, and the optic thalamus was free from any sign of degeneration.

In sections through the crus cerebri, this tract was found to occupy the most mesial portion of the pes cruris, but at this level it was of considerably smaller size than in the anterior limb of the internal capsule. There was also in these sections an obvious degeneration of some of the fibres of the substantia nigra.

In the upper portions of the pons Varolii, the degeneration occupied the same relative position amongst the most mesial of the pyramidal fibres as in the pes cruris, but it was gradually lost to view in the lower parts of the pons. There was no degeneration in the middle cerebellar peduncle on either side.

There was no clear evidence of the passage of degenerated fibres dorsally through the tegment to the region of the third nerve nucleus; and although there was no certain evidence of degeneration in the posterior longitudinal bundles, scattered black dots were usually observed in these tracts.

2. In those cases in which the frontal lobe was extirpated anterior to the pre-central frontal sulcus, a much more extensive degeneration existed in the pes cruris, for not only was there degeneration of the most mesial fibres, as already described, but also of a considerable number of those lying external to them. This was also noted in the pyramidal fibres of the pons.

Our experiments do not throw any new light upon the destination or the function of the efferent frontal fibres. From the fact that the tract diminishes in size as it is traced downwards into the mid-brain, it is evident that fibres are being given off along its course; but we have been unable to confirm the observations of Marinesco (38), who found degeneration in the nucleus caudatus, by Marchi's method, after extirpation of the frontal lobes in monkeys. Some of the fibres of the pre-frontal system were traced into the substantia nigra, where they terminate; an observation which is confirmatory of those of Bechterew (12) and Witkowski (42), who found degeneration and atrophy of this structure in several cases of old-standing lesion of the anterior limb of the internal capsule. The remainder of the fibres of this system pass into the tegmentum pontis, where they terminate probably in relation with the scattered ganglionic cell-groups of this region.

There was no evidence of a direct fronto-cerebellar tract, as the cerebellar peduncles showed no trace of degeneration. If such a connexion exists, it is of an indirect nature through the nucleus pontis; but we have already (p. 32) indicated the existence of a cerebello-cortical system through the superior peduncle, the optic thalamus, and thalamo-cortical afferent system.

The pes cruris may be regarded as consisting of three systems of corticifugal fibres :—

1. The inner, or frontopontine, tract;
2. The outer, or temporopontine, tract; and
3. The middle, or pyramidal, tract.

Although the functions and destination of the last named are well known, the same cannot be said of the two former. What their probable terminations are has been already described. It is evident from the observations recorded in this research, as well as those of FLECHSIG, that each has a complementary corticipetal system from the optic thalamus.

GENERAL SUMMARY.

Beyond describing in the physiological part the symptoms following the different lesions, we have refrained from founding physiological deductions upon the results of the degenerative method, inasmuch as the functions of many of the regions to which the respective tracts of degeneration are capable of being traced are as yet but imperfectly understood, and we do not think that the degenerative method by itself affords a sound basis for physiological conclusions.

The general results of our research may be summarized as follows :—

a. The degenerations of the cerebral portion of the *visual system* showed that it was composed of a corticifugal tract, passing from the occipital lobe, by way of the optic radiations, to the pulvinar thalami of the same side, and to the anterior quadrigeminal body of the same, and partly of the opposite, side :—observations which are in harmony with those of VON MONAKOW. The angular gyrus has no descending or efferent tract to the basal ganglia, but is connected by means of associating fibres with the superior temporal gyrus, the superior and inferior parietal lobule, and the occipital lobe.

A system of corticipetal fibres was traced from the optic thalamus to the angular gyrus and the occipital lobe, in which lobe their distribution was as well marked on the external convolutions as in the cuneus and lips of the calcarine fissure. The distribution of the pulvinar fibres in the occipital lobe and angular gyrus coincided with that of the fibres of the corpus callosum, but there was no means of distinguishing those which were visual from those which were commissural and thalamic.

The angular gyri and occipital lobes are commissurally connected through the

splenium and forceps corporis callosi, in which respect our observations are in harmony with those of VIALET.

b. Inasmuch as the experiments upon the *auditory system* necessitated division of the pedunculus flocculi, the degenerations consequent thereon were first eliminated. These were traced into DEITERS' nucleus, the vermis cerebelli, and tegmentum pontis, corresponding with the observations of BRUCE and STSCHERBACH by the myelination method.

The direct connexions of the *vestibular* division, as shown by section of the eighth nerve trunk distal to the auditory ganglion, are with DEITERS' nucleus and the tegmentum ; while there is also a probable direct connexion with the nucleus of the sixth nerve, as BRUCE has stated.

The connexions of the *cochlear* division, forming the central auditory tract, were found to pass from the accessory auditory ganglion by way of the corpus trapezoides, in association with the lateral fillet, to the internal geniculate body of the opposite side. Thence a tract was found to ascend to the superior temporal gyrus. This is regarded as the corticipetal or cerebral auditory tract. Degeneration was also traced after destruction of the auditory ganglion into both superior olives and posterior quadrigeminal tubercles, chiefly of the opposite side. These results are in confirmation of those of FLECHSIG, KÖLLIKER, HELD, VON MONAKOW, and others, obtained by other methods of investigation.

After destruction of the superior temporal gyrus a tract of degeneration was found to descend to the upper part of the pons Varolii, through the outer fifth of the pes cruris. This constitutes the *temporo-pontine* tract of BECHTEREW and DÉJÉRINE.

The superior temporal gyri are commissurally connected through the forceps of the corpus callosum, and by means of association fibres with the angular gyrus and occipital lobe.

c. In some cases of lesion of the tegment there was no obvious loss of cutaneous sensibility, while in others this was pronounced.

These latter were lesions involving the reticular formation of the pons and crus. In both cases, however, corticipetal degenerations were induced. These were traced through both limbs of the internal capsule, the external capsule, and the centrum ovale to the cerebral cortex, both on the convexity and mesial aspect, including the gyrus fornicatus. This corticipetal system is less extensive in the frontal than in the other regions of the cerebrum. It would seem to harmonise with the thalamic corticipetal fibres, which FLECHSIG has recently described as the first, second, and third "sensory" systems, ascending respectively to the Rolandic area, the falciform lobe, the frontal region, and gyrus fornicatus, myelinating at different periods.

Many of the fibres of the tegmentum appear to pass through the optic thalamus without ending in it, while others terminate in this ganglion. This is shown by the fact that destruction of the lateral and ventral parts of the optic thalamus led to a more extensive degeneration than that following destruction of the tegmentum alone,

the fibres degenerating towards the same cortical regions. But we have not been able to distinguish, by the degenerative method, between those of sensation proper and other afferent fibres which ascend to the cortex in this region.

Many fibres from the optic thalamus were found to cross by the corpus callosum to the opposite cerebral hemisphere, thus supporting the view of HAMILTON that this structure is a decussation as well as a commissure. Our observations show that the decussation is of thalamic corticipetal fibres.

d. The other *afferent cranial nerves*, which were made the subject of experiment, were the sensory division of the trigeminus and the glossopharyngeus, which were divided proximal to their ganglia.

Apart from degeneration of the so-called ascending trigeminal and glossopharyngeal roots, traceable as far as the spinal-medullary junction, no evidence was obtained as to their central connexions.

e. The results of experiments upon the *pre-frontal* and *post-frontal* areas confirmed the existence of a *fronto-pontine* tract, which descends through the anterior limb of the internal capsule and inner portion of the pes cruris to the pons Varolii, observations which harmonise with the previous ones of FERRIER, as well as of BRISSAUD and BECHTEREW. The experiments, however, did not throw any new light upon the destination or function of the efferent frontal fibres.

TABULAR Statement of the Experiments referred to in the text.

No. of Experiment.	Nature of Experiment.	Operation.	Killed.
1	Removal of occipital lobe (left side) .	February 18, 1896	March 18, 1896
2	" " " " " . .	" 26, 1896	" 25, 1896
3	" " " " " . .	November 9, 1896	November 16, 1896
4	Division of splenium corporis callosi .	" 20, 1894	January 16, 1895
5	Destruction of angular gyrus (left side)	December 3, 1895	" 8, 1896
6	" " " " "	April 24, 1896	May 2, 1896
7	Destruction of pulvinar thalami (left side)	November 20, 1894	January 16, 1895
8	Extirpation of frontal lobes and angular gyri	1st, May 28, 1895; 2nd, June 18, 1895	June 21, 1895
9	Division of eighth nerve distal to accessory ganglion	March 6, 1894	July 10, 1894
10	Division of eighth nerve distal to accessory ganglion	May 1, 1894	May 19, 1894
11	Division of eighth nerve proximal to ganglion	November 6, 1895	November 12, 1895
12	Division of eighth nerve proximal to ganglion	February 4, 1896	February 26, 1896
13	Destruction of posterior quadrigeminal body (left side)	" 18, 1896	March 18, 1896
14	Destruction of internal geniculate body (left side)	" 26, 1896	" 25, 1896
15	Destruction of internal geniculate body (left side)	January 12, 1897	February 10, 1897
16	Destruction of superior temporal gyrus (left side)	" 28, 1896	" 26, 1896
17	Destruction of superior temporal gyrus (left side)	December 1, 1896	January 6, 1897
18	Amputation of flocculus	July 28, 1894	August 21, 1894
19	" " "	May 1, 1896	June 2, 1896
20	Division of sensory root of trigeminus	February 28, 1893	May 8, 1893
21	Division of glossopharyngeal roots . .	June 4, 1894	June 11, 1894
22	Hemisection of tegmentum pontis . .	February 13, 1894	February 20, 1894
23	" " " " . .	October 9, 1894	October 13, 1894
24, 25	Hemisection of tegmentum cruris, two cases	Same as internal geniculate body.	
26	Extirpation of pre-frontal lobe (left side)	May 14, 1894	June 18, 1894
27	Extirpation of pre-frontal lobe (left side)	November 9, 1894	December 5, 1894
28	Extirpation of pre-frontal lobe (left side)	June 3, 1893	July 15, 1893
29	Extirpation of frontal lobe (left side) .	December 1, 1894	December 25, 1894
30	Extirpation of frontal lobes (bilateral)	1st, Nov. 9, 1894; 2nd, Dec. 11, 1894	January 17, 1895

BIBLIOGRAPHY.

1. FERRIER. Croonian Lectures, 1891, pp. 47, 48.
2. HENSCHEN. Path. des Gehirns. Upsala, 1893.
3. SHAW and THOMPSON. Brit. Med. Journ., Sept., 1896.
4. SACHS. Das Hemisphärenmark. Breslau, 1892.

5. MURATOFF. Neurol. Centralbl., 1893.
6. VON MONAKOW. Arch. f. Psych., vols. 20, 22.
7. VIALET. Centres Cérébraux de la Vision. Paris, 1893.
8. FLECHSIG. (*a*) Die Localisation der geistigen Vorgänge, 1896; (*b*) Neurol. Centralbl., 1897, p. 295.
9. DÉJÉRINE. Société de Biologie, May, 1892.
10. BEEVOR. Phil. Trans., B, 1891, p. 135.
11. BRUCE. Tracts of Mid and Hind Brain. Edinb., 1892.
12. BECHTEREW. Die Leitungsbahnen, 1894.
13. STSCHERBACH. Neurol. Centralbl., 1893, p. 227.
14. EDINGER. Vorlesungen, 1896, p. 360.
15. FERRIER and TURNER. Phil. Trans., B, 107, 1894.
16. BOYCE. Phil. Trans., B, 121, 1895.
17. VON KÖLLIKER. (*a*) Die Gewebelehre, 1893, vol. 1; (*b*) ditto, 1896, vol. 2, p. 396.
18. HELD. Arch. f. Anat. und Physiol., 1891 and 1893.
19. BRUCE. Proc. Roy. Soc. Edinb., 1889.
20. FLECHSIG. Neurol. Centralbl., 1895, p. 547.
21. BAGINSKY. VIRCHOW'S Archiv, 1886, and Bd. 119.
22. VON MONAKOW. Arch. f. Psych., Bd. 22, p. 7.
23. BUMM. Reference in EDINGER, *op. cit.* (14).
24. BECHTEREW. Neurol. Centralbl., 1885, p. 398.
25. ROSSOLYMO. Neurol. Centralbl., 1886, p. 47.
26. ZACHER. Arch. f. Psych., Bd. 22, p. 654.
27. DÉJÉRINE. Bull. Société de Biologie, 1894.
28. FERRIER. Brain, 1894, p. 21.
29. TURNER, W. A. (*a*) Brit. Med. Journ., Nov., 1895; (*b*) Brain, 1895, p. 231.
30. WALLENBERG. Referred to by EDINGER, Vorlesungen, 1896.
31. EDINGER. (*a*) Anat. Anzeig., 1887, p. 27; (*b*) Vorlesungen, 1896, p. 366.
32. STARR. Journal of Nerv. and Mental Dis., 1884.
33. MOELI and MARINESCO. Arch. f. Psych., 1892, p. 655.
34. FLECHSIG and HÖSEL. Neurol. Centralbl., 1890, No. 14.
35. VON MONAKOW. Referred to by BECHTEREW, Leitungsbahnen, p. 158.
36. MOTT. Brain, 1895, p. 11.
37. FRANCE. Phil. Trans., B, 1889, p. 331.
38. MARINESCO. Comptes Rendus, Société de Biologie, 1895.
39. HITZIG. Arch. f. Psych., vol. 15, p. 270.
40. HAMILTON. (*a*) Proc. Roy. Soc. Lond., 1884, p. 349; (*b*) Text-book, vol. 2, Part 2, p. 645.
41. HORSLEY and SCHÄFER. Phil. Trans., B, 1888.
42. WITKOWSKI. Referred to by BECHTEREW, *op. cit.* (12).

DESCRIPTION OF THE PLATES.

We are indebted to Mr. J. E. BARNARD for the photo-micrographs, which have been taken direct from our original sections.

PLATE 1.

Fig. 1. The left cerebral hemisphere from Exp. 5, showing the extent of destruction of the angular gyrus. The lesion in Exp. 6 was of similar extent. In both, the lesion was accurately limited, and there was no involvement of any other part of the brain.

Fig. 2 represents the amount and extent of the lesions in Exp. 8. Both frontal lobes and angular gyri have been removed. On the left side the lesion of the frontal lobe extends right up to the pre-central sulcus, and its vertical prolongation to the longitudinal fissure; on the right side the extirpation has not been so complete. The lesion of the angular gyrus on the left side has extended slightly into the superior parietal lobule, but is accurately defined on the right side.

Fig. 3 is a photograph of the left cerebral hemisphere of Exp. 29, showing the extent of the removal of the frontal lobe.

Fig. 4 is a frontal section through the anterior quadrigeminal region, showing the lesion on the left side which occasioned anæsthesia and analgesia of the opposite side of the body (text, p. 28). *x*, site of the lesion; *py.*, pyramid or pes cruris; *a.c.q.*, anterior quadrigeminal body; *o.tr.*, optic tract; *o.ch.*, optic chiasma; *aq.Sy.*, aqueductus Sylvii.

Fig. 5 represents the frontal extremity of the brain of Exp. 26, showing the extent of removal of the left pre-frontal region. The extirpation was the same in Exps. 27 and 28.

Figs. 6 and 7 are photographs of the left cerebral hemispheres from Exps. 16 and 17, by which is shown the lesion of the superior temporal convolution. That illustrated by fig. 7 is more extensive than in fig. 6.

PLATE 2.

N.B.—The figures on this plate are photo-micrographs of sections stained by the MARCHI method, except fig. 6, which is a WEIGERT preparation. Degenerated fibres are represented as *black* lines or dots in the figures.

Fig. 1 is from a frontal section through the pons Varolii at the level of the corpus trapezoides from a case in which the accessory auditory ganglion was

destroyed (Exp. 12). On the left side—side of lesion—the degeneration is compact, but after crossing the raphé spreads out in a fan shape. A few scattered trapezoid fibres are seen in the pyramids and in the tegmentum (text, p. 16).

Fig. 2 shows a part of the posterior horn in the occipital lobe. The semilunar area containing degenerated fibres in the centre of the figure is part of the forceps corporis callosi. The degeneration is that resulting from division of the splenium corporis callosi (text, p. 8).

Fig. 3 is a section through the outer part of the lateral region of the optic thalamus and posterior limb of the internal capsule, showing the degeneration of corticipetal fibres passing from the optic thalamus through the *Gitterschicht* into and up the internal capsule on their way to the cortex cerebri after lesion of the optic thalamus (text, p. 30). The optic thalamus forms the upper, the internal capsule the lower, part of the figure.

Fig. 4 is a portion of the tegmentum cruris mesial to the internal geniculate body from a case (Exp. 12) in which the accessory auditory ganglion was destroyed. The large black dots scattered over the field represent the fibres in this situation, which were found degenerated. They represent the peduncular portion of the central auditory tract on the side opposite the lesion (text, p. 18).

Fig. 5 is from a section taken through the anterior quadrigeminal region, and shows the fibres of the "middle zone," which degenerate after extirpation of the occipital lobe of the same side. These fibres are observed entering at the left-hand side, and passing towards the middle line on the right of the figure (text, p. 7).

Fig. 6 is a frontal section through the cerebrum of a monkey, in which the pulvinar thalami and adjacent part of the optic thalamus was destroyed (Exp. 7; text, p. 6). The lesion is seen immediately to the left of the middle line, and shows almost complete destruction of this part of the optic thalamus.

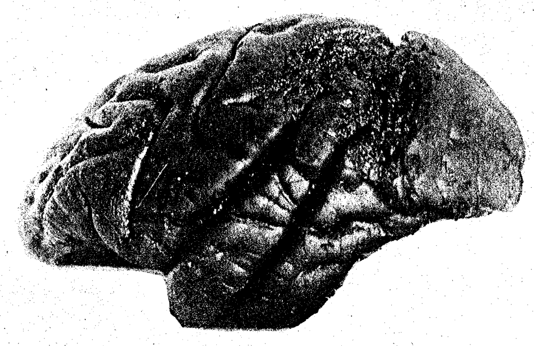


Fig. 1.

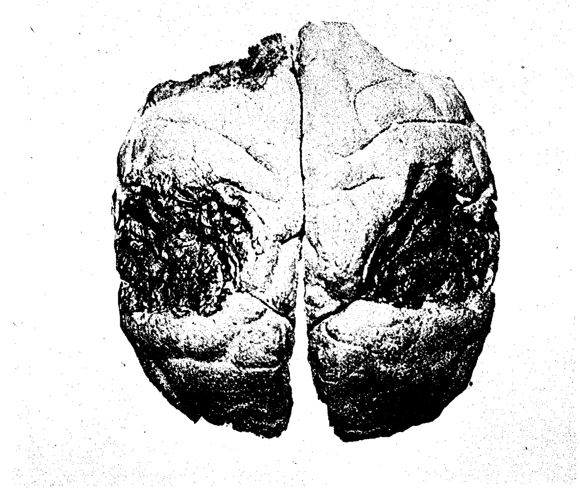


Fig. 2.

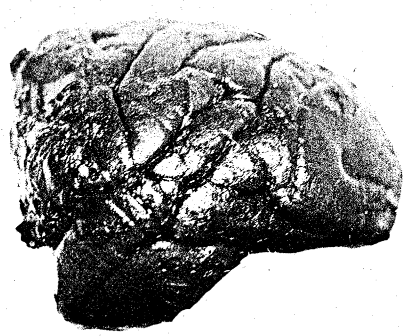


Fig. 3.

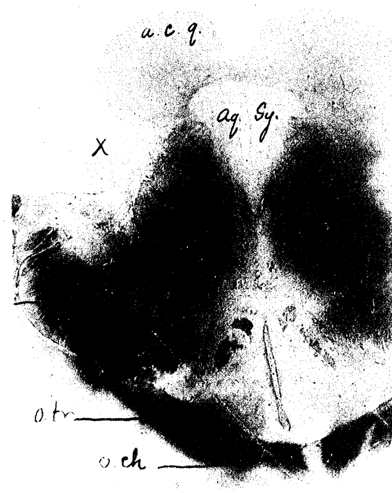


Fig. 4.

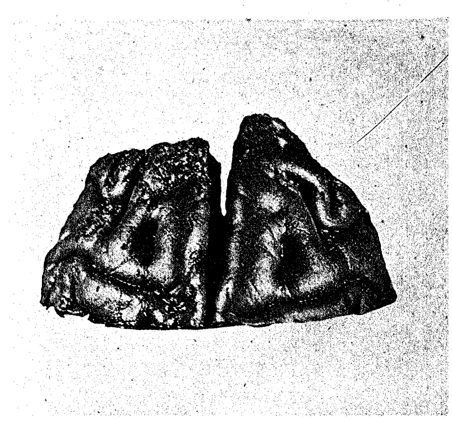


Fig. 5.

Fig. 6.

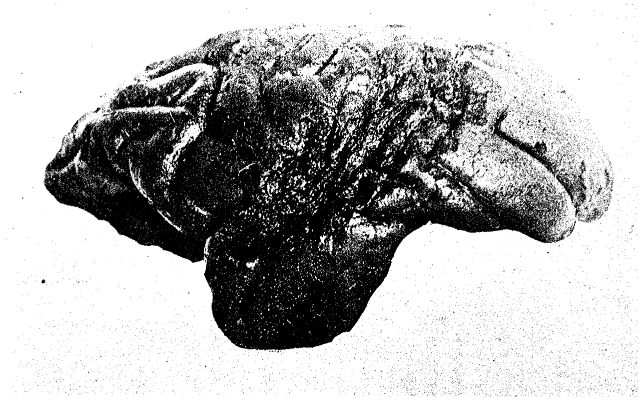


Fig. 7.

S. B. Bolas and Co., Collotype.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

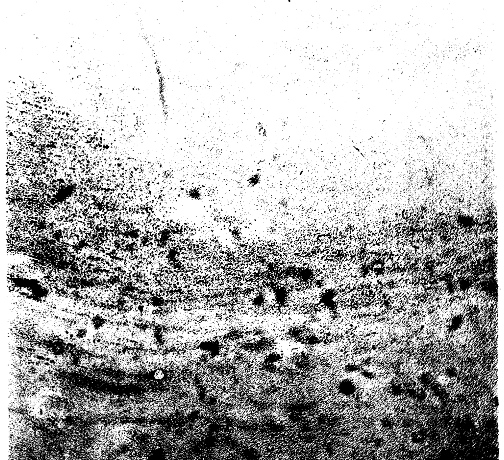


Fig. 5.

Fig. 6.

S. B. Bolas and Co., Collotype.

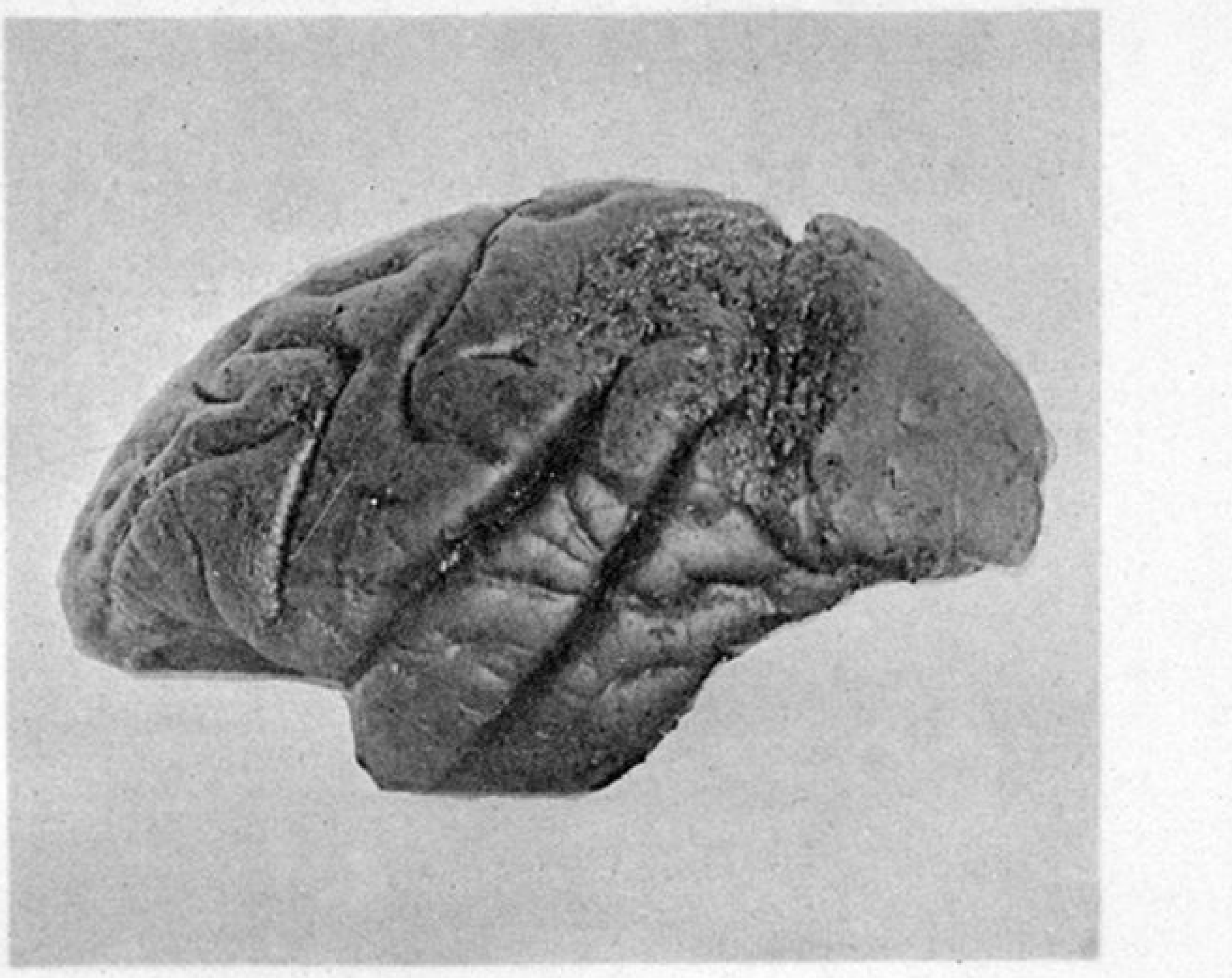


Fig. 1.

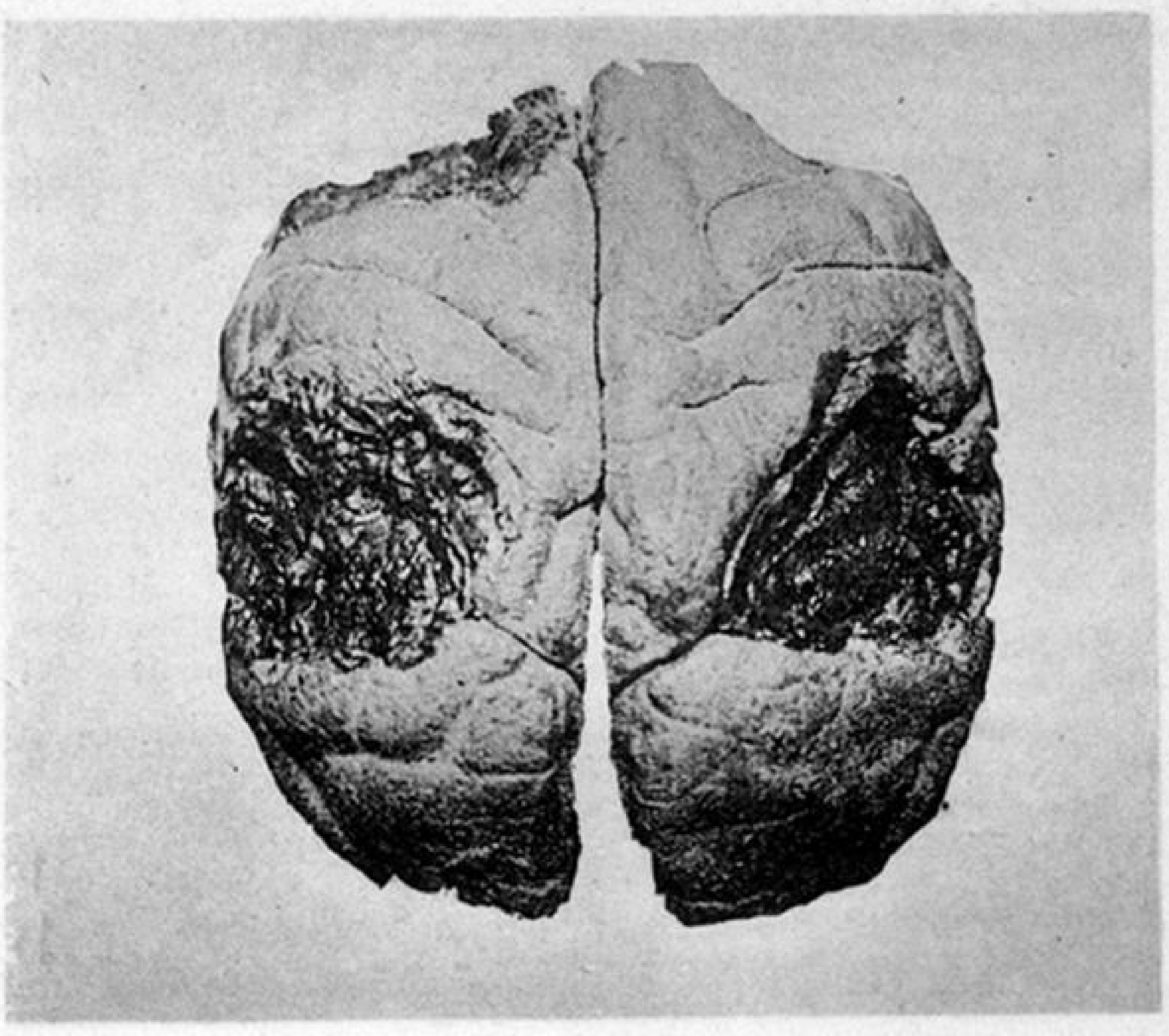


Fig. 2.

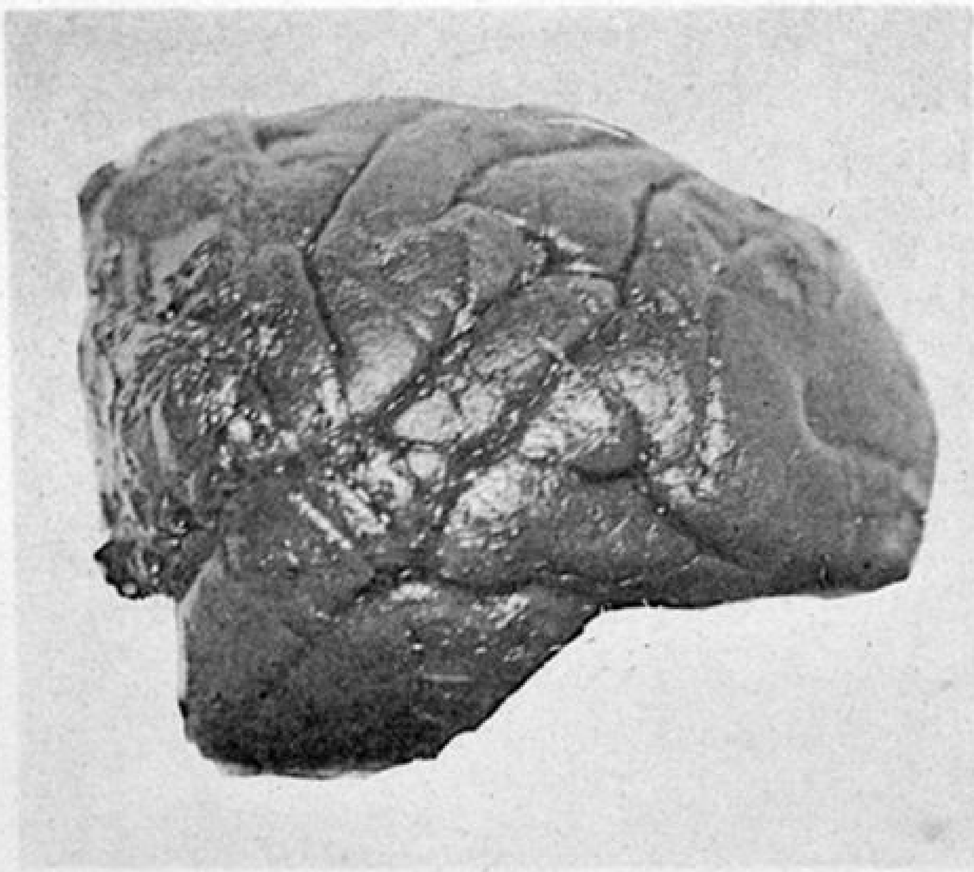


Fig. 3.

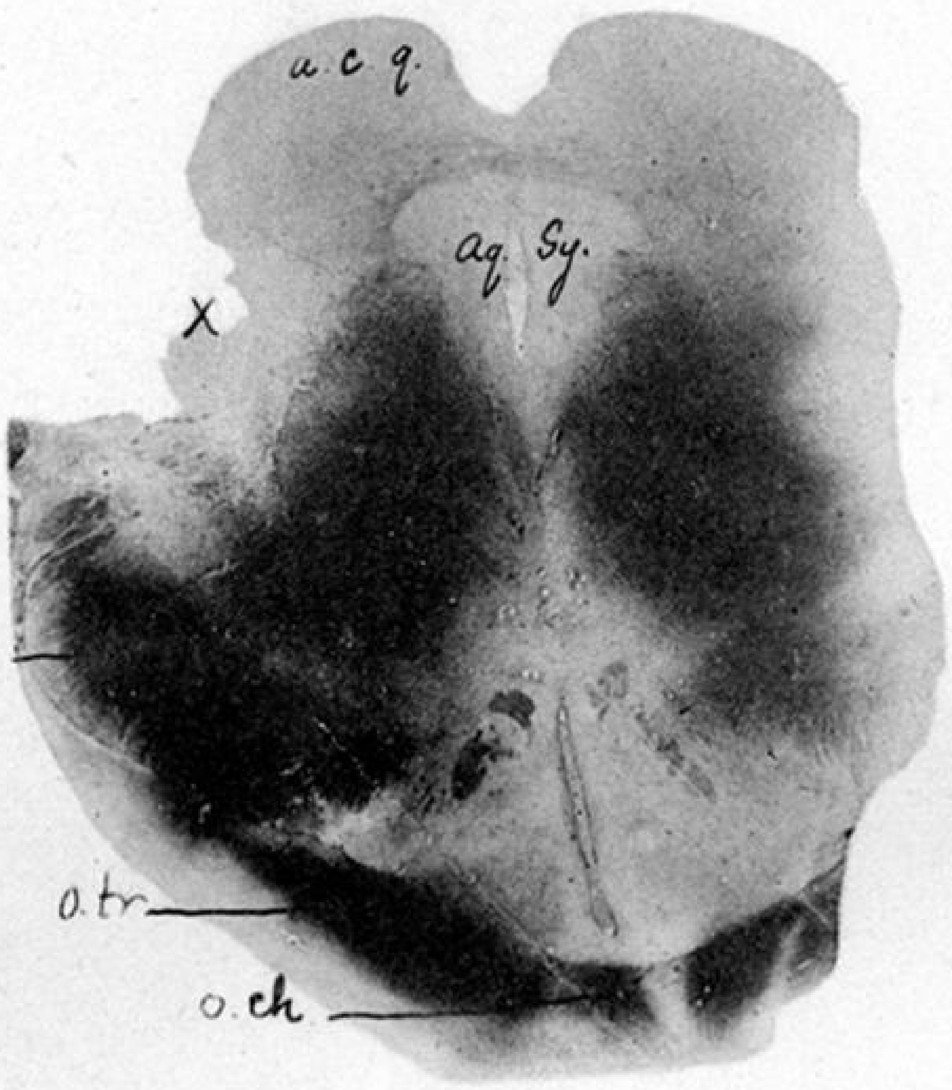


Fig. 4.

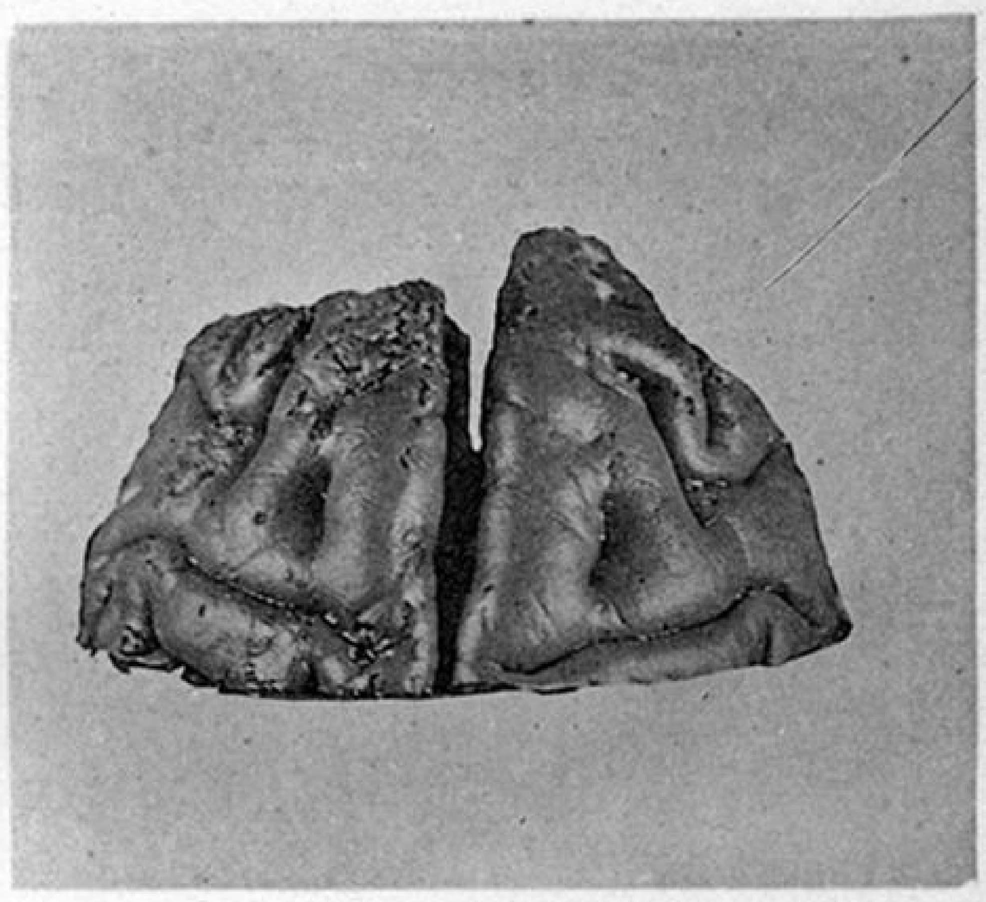


Fig. 5.

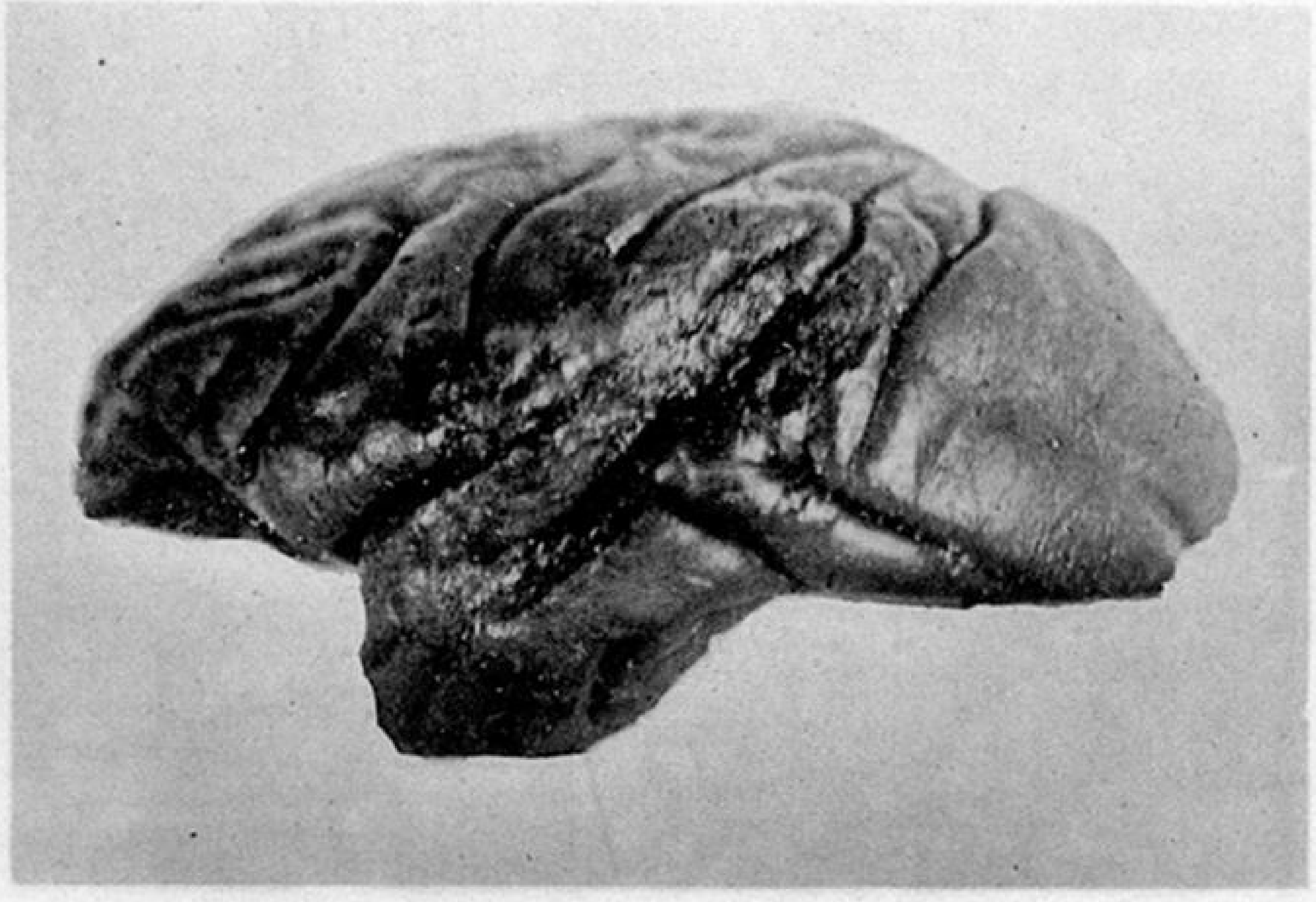


Fig. 6.

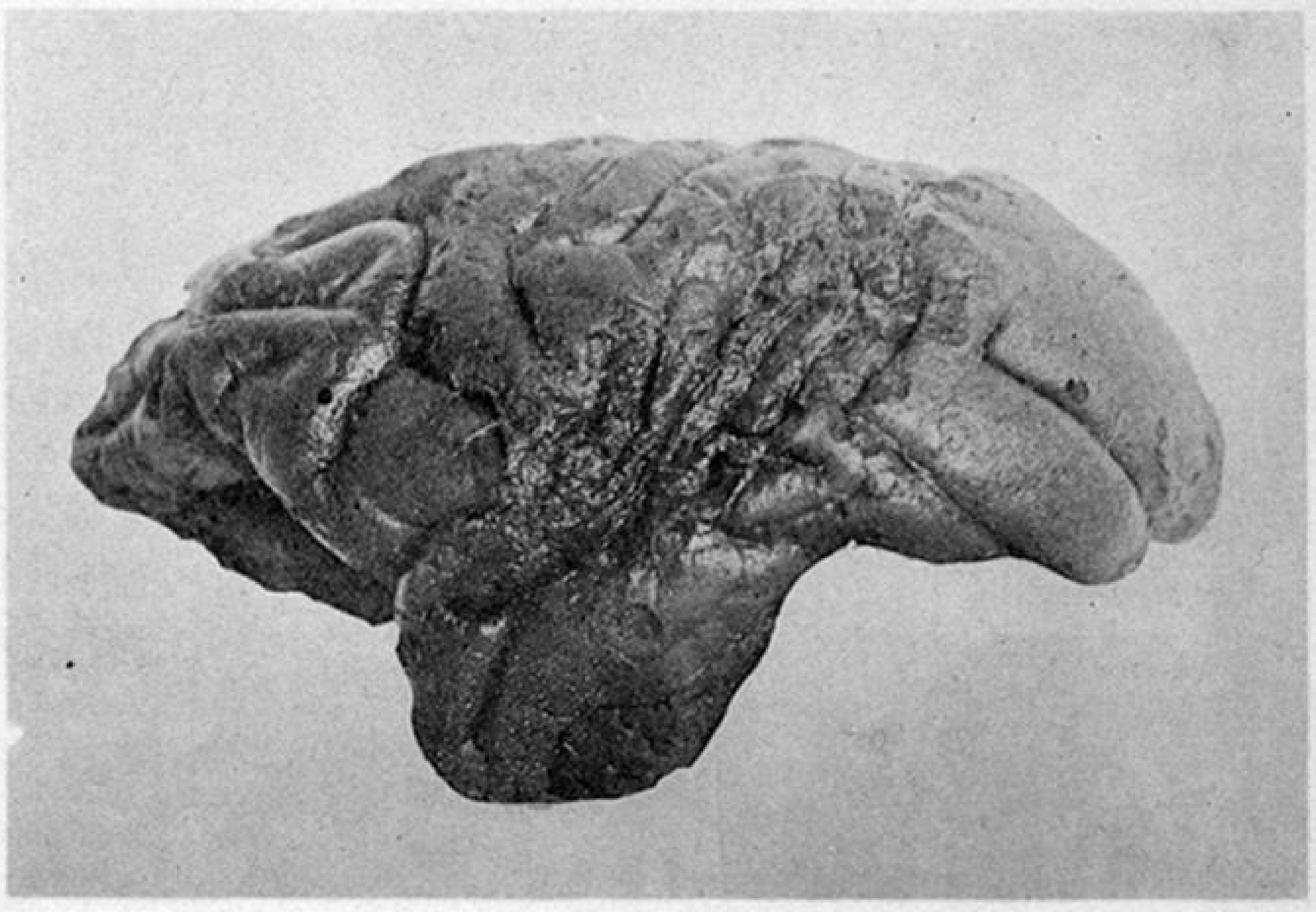


Fig. 7.

PLATE 1.

Fig. 1. The left cerebral hemisphere from Exp. 5, showing the extent of destruction of the angular gyrus. The lesion in Exp. 6 was of similar extent. In both, the lesion was accurately limited, and there was no involvement of any other part of the brain.

Fig. 2 represents the amount and extent of the lesions in Exp. 8. Both frontal lobes and angular gyri have been removed. On the left side the lesion of the frontal lobe extends right up to the pre-central sulcus, and its vertical prolongation to the longitudinal fissure; on the right side the extirpation has not been so complete. The lesion of the angular gyrus on the left side has extended slightly into the superior parietal lobule, but is accurately defined on the right side.

Fig. 3 is a photograph of the left cerebral hemisphere of Exp. 29, showing the extent of the removal of the frontal lobe.

Fig. 4 is a frontal section through the anterior quadrigeminal region, showing the lesion on the left side which occasioned anæsthesia and analgesia of the opposite side of the body (text, p. 28). *x*, site of the lesion; *py.*, pyramid or pes cruris; *a.c.q.*, anterior quadrigeminal body; *o.tr.*, optic tract; *o.ch.*, optic chiasma; *aq.Sy.*, aqueductus Sylvii.

Fig. 5 represents the frontal extremity of the brain of Exp. 26, showing the extent of removal of the left pre-frontal region. The extirpation was the same in Exps. 27 and 28.

Figs. 6 and 7 are photographs of the left cerebral hemispheres from Exps. 16 and 17, by which is shown the lesion of the superior temporal convolution. That illustrated by fig. 7 is more extensive than in fig. 6.

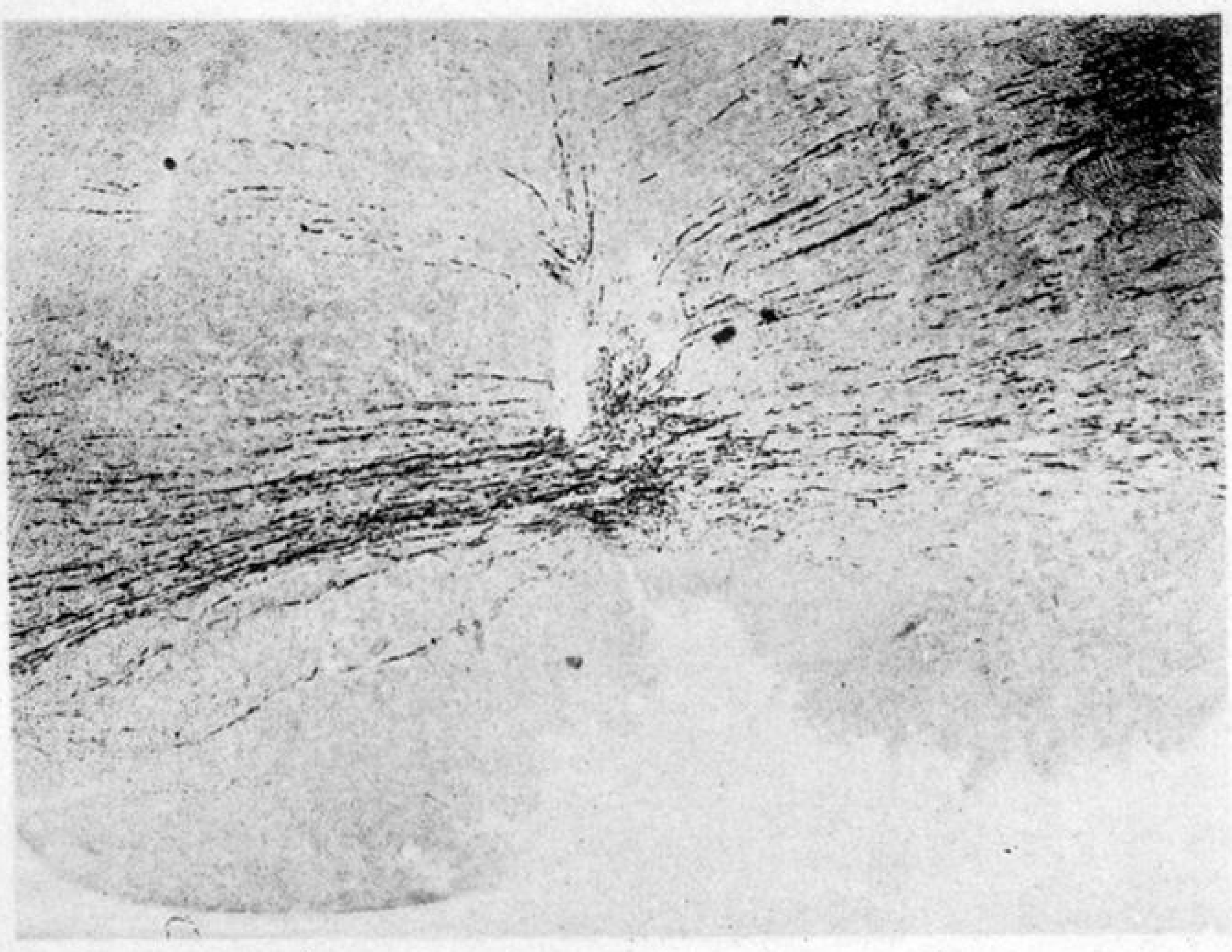


Fig. 1.

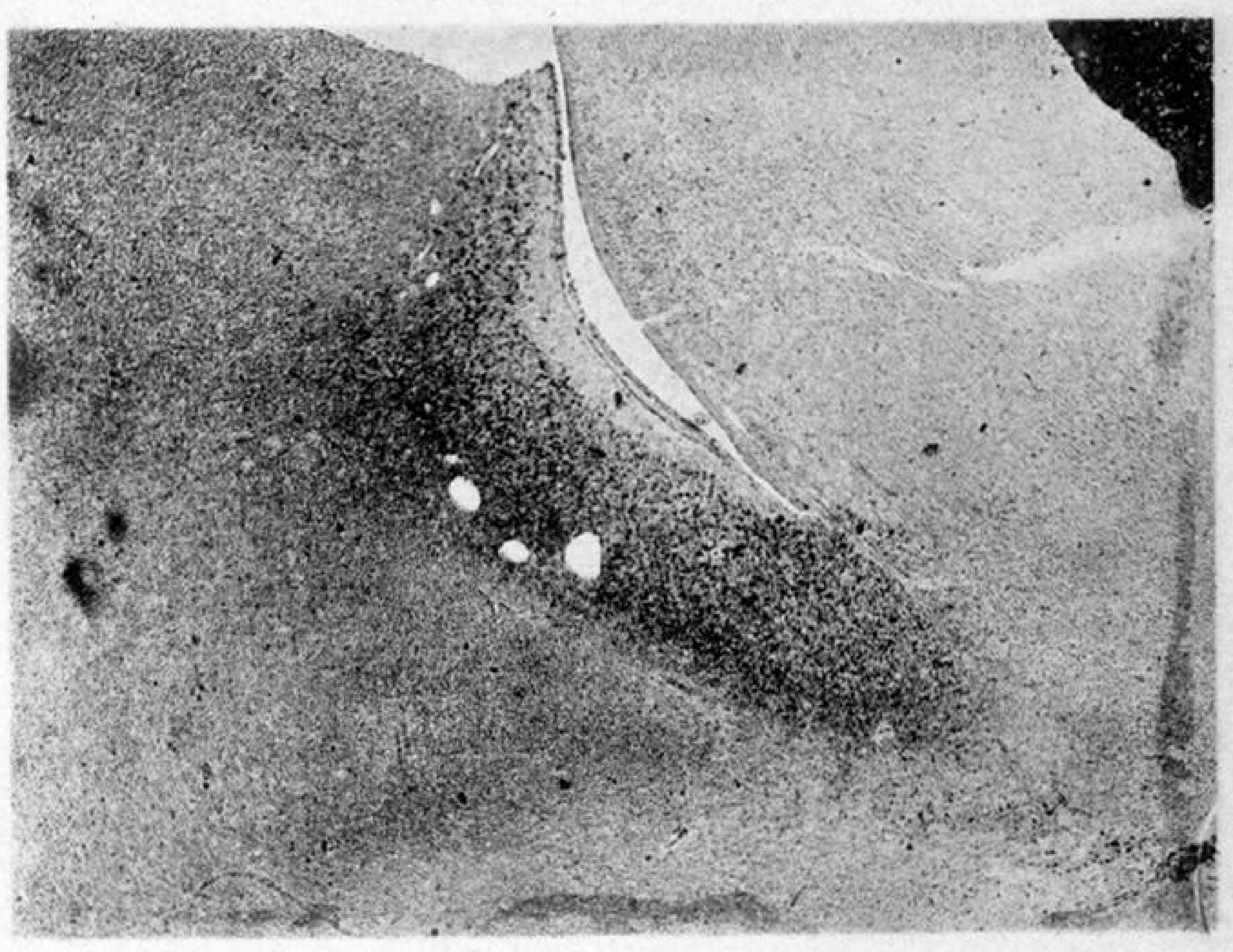


Fig. 2.

Fig. 3.

Fig. 4.

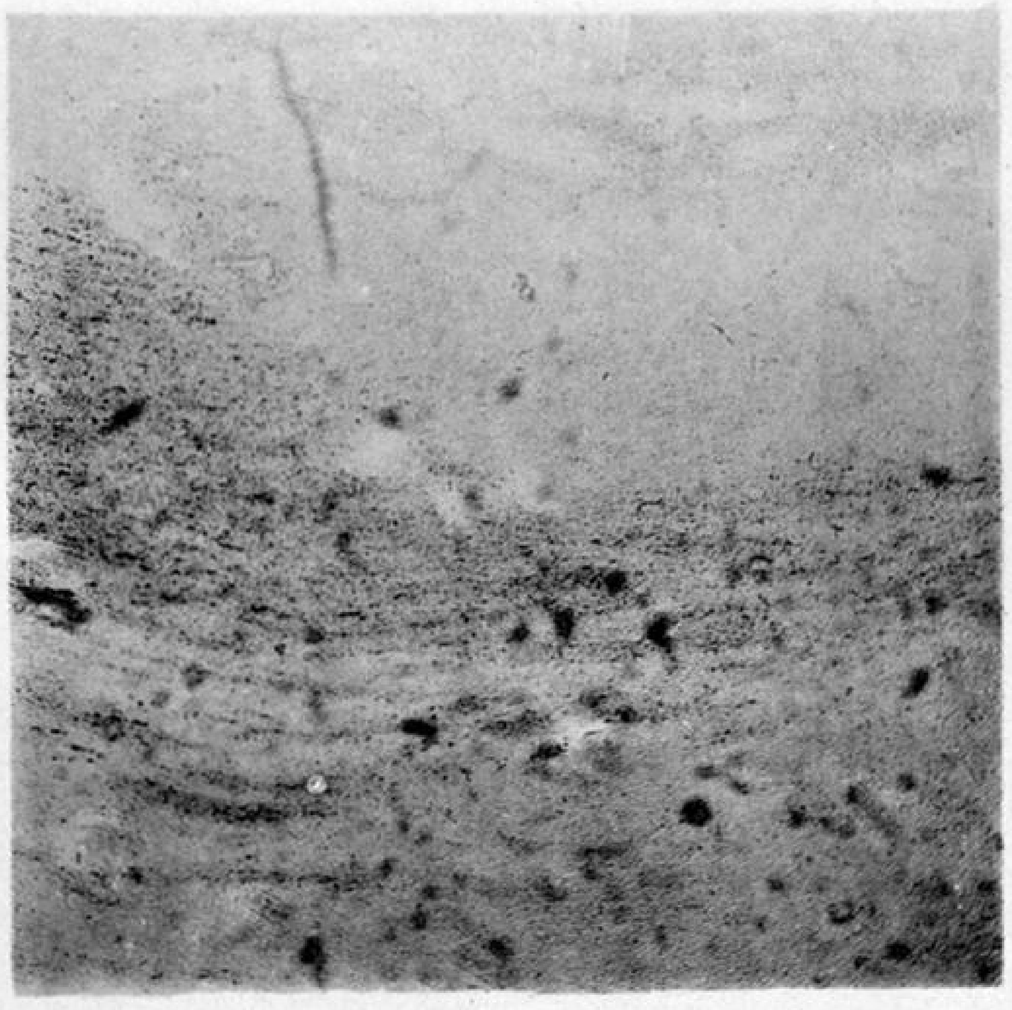


Fig. 5.

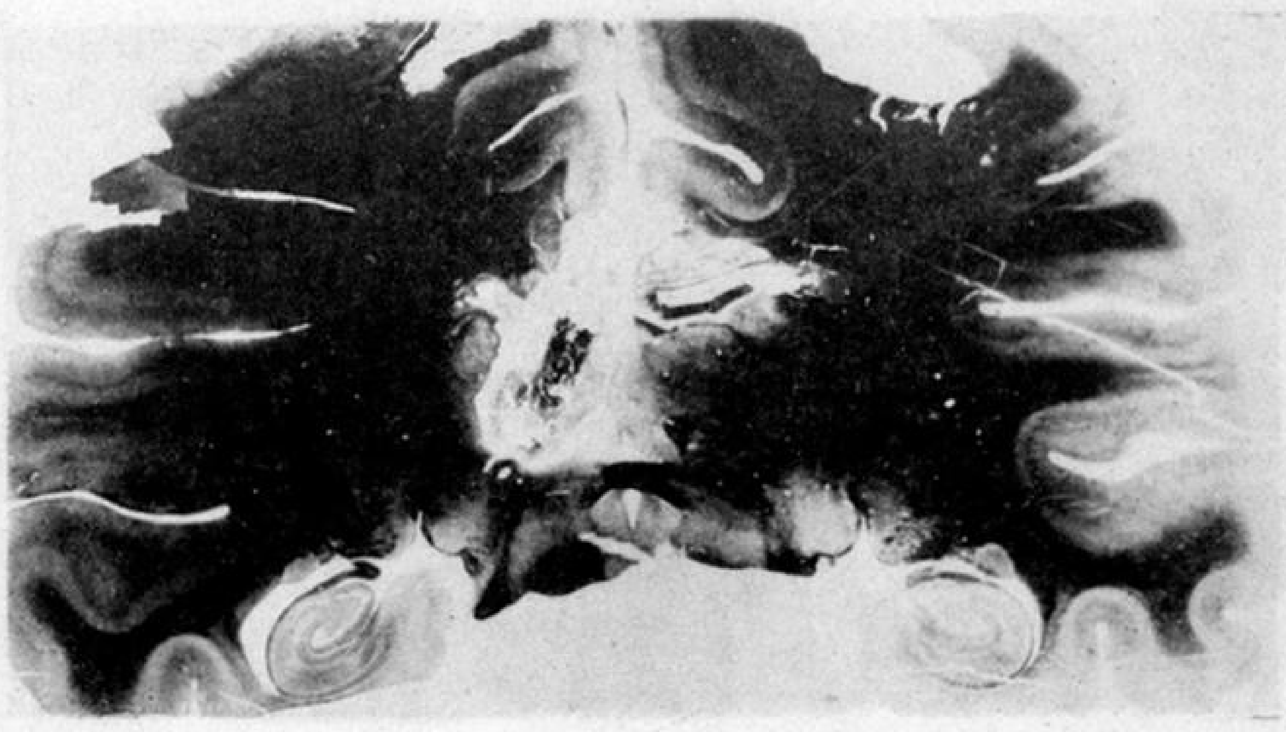


Fig. 6.

PLATE 2.

N.B.—The figures on this plate are photo-micrographs of sections stained by the MARCHI method, except fig. 6, which is a WEIGERT preparation. Degenerated fibres are represented as *black* lines or dots in the figures.

Fig. 1 is from a frontal section through the pons Varolii at the level of the corpus trapezoides from a case in which the accessory auditory ganglion was destroyed (Exp. 12). On the left side—side of lesion—the degeneration is compact, but after crossing the raphé spreads out in a fan shape. A few scattered trapezoid fibres are seen in the pyramids and in the tegmentum (text, p. 16).

Fig. 2 shows a part of the posterior horn in the occipital lobe. The semilunar area containing degenerated fibres in the centre of the figure is part of the forceps corporis callosi. The degeneration is that resulting from division of the splenium corporis callosi (text, p. 8).

Fig. 3 is a section through the outer part of the lateral region of the optic thalamus and posterior limb of the internal capsule, showing the degeneration of corticipetal fibres passing from the optic thalamus through the *Gitterschicht* into and up the internal capsule on their way to the cortex cerebri after lesion of the optic thalamus (text, p. 30). The optic thalamus forms the upper, the internal capsule the lower, part of the figure.

Fig. 4 is a portion of the tegmentum cruris mesial to the internal geniculate body from a case (Exp. 12) in which the accessory auditory ganglion was destroyed. The large black dots scattered over the field represent the fibres in this situation, which were found degenerated. They represent the peduncular portion of the central auditory tract on the side opposite the lesion (text, p. 18).

Fig. 5 is from a section taken through the anterior quadrigeminal region, and shows the fibres of the "middle zone," which degenerate after extirpation of the occipital lobe of the same side. These fibres are observed entering at the left-hand side, and passing towards the middle line on the right of the figure (text, p. 7).

Fig. 6 is a frontal section through the cerebrum of a monkey, in which the pulvinar thalami and adjacent part of the optic thalamus was destroyed (Exp. 7; text, p. 6). The lesion is seen immediately to the left of the middle line, and shows almost complete destruction of this part of the optic thalamus.