VI. A Contribution to the Study of Descending Degenerations in the Brain and Spinal Cord, and of the Seat of Origin and Paths of Conduction of the Fits in Absinthe Epilepsy.

By Rubert Boyce, M.B., Professor of Pathology, University College, Liverpool.

Communicated by Professor V. Horsley, F.R.S.

Received February 8,—Read March 15, 1894.

(From the Pathological Laboratory, University College, London.)

[Plate 3.]

This investigation was undertaken at the suggestion of Professor Horsley, in order to determine the seat of origin of the fits in absinthe epilepsy and to find out what share the motor cortex or other portion of the cerebral hemisphere, the basal ganglia, cerebellum, or the centres in the medulla and spinal cord, might take in the production of the fit.

For this purpose numerous lesions were made both in the brain and spinal cord of the cat, and absinthe administered immediately after, or after the lapse of days or weeks. The results of the absinthe stimulation were recorded by the graphic method.

The following is the list of lesions:—

- I. Lesions after which animals were kept alive
- 1. Removal of a complete cerebral hemisphere in 40 cats.
- 2. Removal of motor area only, 4 cats.
- 3. Division of crus cerebri in 2 cats.
- 4. Removal of a lobe of cerebellum in 12 cats.
- 5. Hemisection of spinal cord in 4 cats.
- II. Lesions after which animals were not kept alive for any length of time.
- 1. The preceding operations.
- 2. Removal of both cerebral hemispheres.
- 3. Removal of cerebellum.
- 4. Removal of one cerebral hemisphere and opposite lobe of cerebellum, &c., &c.
- 5. Removal of one hemisphere and division of opposite half of the spinal cord.

MDCCCXCV.--B.

2 T

29,4.95.

The large amount and variety of material arising from these experiments furnished the basis of an anatomical investigation, by the *Marchi method*, of more especially the centrifugal paths in the brain and cord.

In order to enable a clearer comparison to be made between the various results obtained by the experimental and anatomical methods, the paper is divided into—

- I. The anatomical changes.
- II. Behaviour of the animal during life.
- III. Results of absinthe excitation.
- IV. Conclusions.

PART I.—ANATOMICAL CHANGES.

Microscopic Technique.—The tissues were hardened for about ten days in Müller's fluid, and then thin slices transferred to Marchi's solution of osmic acid in Müller's fluid. In this solution the slices remained for a fortnight or longer, great care being taken to prevent the loss of the osmic acid by evaporation, and to renew it when it became weak. The slices did not exceed the $\frac{1}{12}$ in. in thickness. It was found that the osmic acid penetrated better when the tissues had been thoroughly hardened in Müller's fluid, very good results even being obtained after one year's hardening.

After the action of the osmic acid, the slices were dehydrated and embedded in collodion and cut under alcohol. The sections were clarified in xylol-phenol and mounted in Canada balsam. My experience has shown that mere time (up to two years) has not had any serious solvent action upon the myelin which has reacted with the osmic acid, but the latter appears to slowly diffuse from the rest of the nerve tissue, the sharply differential anatomical outlines of the recently-mounted section becoming soon lost. These differences will be readily appreciated in the photographs.

The Marchi Reaction.—I have observed commencing signs of the black reaction as early as the 4th day in the vicinity of the wound. On the 5th day there is a little extension, and this increases to the 10th day, when the degenerative reaction is extensive. From the 14th day onwards, to weeks, or two or three months, I have not observed in the cat any marked extension of the degeneration.

Numerous objections have been raised against the Marchi method, chiefly on the ground that it stains too much, the reaction attacking the healthy nerve-fibres. But a long, straight, healthy, darkly-stained nerve-fibre, if present, can be readily distinguished from the varicose and broken up, black, degenerated fibre; I have found the former very rare in my preparations. It is said that some nerve tracts and nerve roots may normally give the black reaction, but this I cannot confirm in the cat. When, in the cord, a hemisection is made, only the tracts upon the same side, and a few fibres upon the opposite side, degenerate; yet I have seen cases where, after the operation, there has been considerable change upon the opposite side; but in these cases the cause could be readily demonstrated in the complete traumatic myelitis at the seat of lesion. In many of Marchi's own cases, which have been characterised

by most marked, wide spread change in various directions, I think that a similar explanation must be sought. It is possible that the fibres react more readily in some animals than in others, but of this we will be able to judge better after more extended observation. In my own preparations the accuracy of this beautiful method of demonstrating degenerate paths rests upon the following data:—1. There is no trace of reaction in normal cats' cords, or in cords before the fourth day after the lesion. I have verified this in numerous cases. 2. The degeneration is strictly limited to definite anatomical groups of fibres. 3. In the case of bilateral tracts, the degeneration is confined to one tract in the case of unilateral lesion. 4. The marked uniformity of the results obtained in each group of experiments.

1. The Degenerations Resulting from the Removal of One Hemisphere in the Cat.

In all thirty-five cases were examined, the material being furnished by animals which had lived, for varying periods, from two days to three months after the operation.

Description of Operation.—Under the usual precautions of complete anæsthesia and asepsis, a considerable portion of the left* hemisphere was laid bare. After the arrest of oozing, the dura was freely incised, and a blunt pointed bistoury passed forward between the hemispheres to the frontal bone; the knife was then carried backwards, passing vertically through corpus callosum and ventricle; close to the tentorium the knife was carried outwards dividing the crus cerebri flush with the tentorium. The hemisphere was then removed and bleeding arrested by cotton sponges, rinsed out of very hot sterilised water, or normal saline. In other cases, and with, perhaps, better success, the hemisphere was removed in several pieces, use being made of the scoop and scissors to facilitate the complete removal of the brain-substance. The bleeding is sometimes very great. The wound is closed by catgut or silk ligatures, and protected by boracic acid, wood wool, and collodion. In the first two cases artificial respiration had to be resorted to.

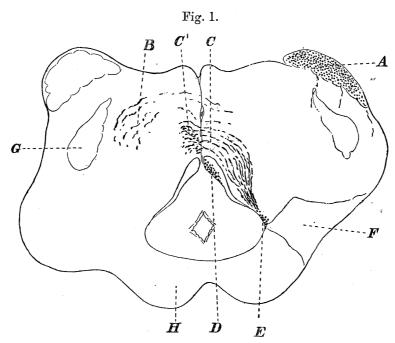
Apart from the washing of the skin with corrosive sublimate, no antiseptics were used, reliance was placed on sterilised water or saline solution. Experience dearly purchased showed that traces of carbolic acid applied to the interior of the skull resulted in irritation and the death of the animal.

If any signs of pressure were manifest the wound was opened and the cavity washed out with warm boracic acid.

Examination of the brain after death, or after hardening, showed that the division was mesial, or very nearly so; that the caudate and lenticular nucleus and the optic thalamus, with the exception, in some cases, of its most posterior part, were removed; that the optic tract was divided. Adhering to the cut surface of the right hemisphere, there was a certain amount of very soft repair tissue mixed with blood clots.

^{*} In this operation the left hemisphere has always been removed.

The posterior incision through the crus cerebri amounted to a hemisection of the mesencephalon in the region of the corpora quadrigemina, aqueduct of Sylvius, and third nerves. The lesion in the majority of cases penetrated externally a little lower than the level of exit of the third nerves, but as the latter are situated very mesially they usually escaped injury. In one case the results of the lesion were found as low as the commencement of the ascending root of the Vth nerve. The incision usually passed between the anterior and posterior corpus quadrigeminum, then extended into the aqueduct beneath, and passed forwards and outwards through the tegmentum



Transverse section passing through anterior corpora quadrigemina and Meynert's decussation. F, lower end of wound made by the hemisection through the mesencephalon on the left side; A, degenerate and atrophied pyramid (left); B, Forel's decussating fibres commencing to form the lateral columnar tract; C, C', Meynert's decussating fibres commencing to form the antero-lateral columnar fibres; D, degenerate posterior longitudinal bundle fibres (anterior columnar fibres); E, degenerate descending root of Vth; G, Lemniscus; H, ant. corp. quad.

(usually avoiding the third nerve), through the outer part of the red nucleus, the outer part or whole of the fillet, and the outer part of the crusta. The line of incision also penetrated obliquely downwards as well as outwards. The origin of the descending root of the Vth in the grey matter in the side of the aqueduct was invariably injured. These points will be rendered clear by the figures.

Mesencephalon,* immediately below the level of the IIIrd nerve (fig. 1). The

^{*}In the following anatomical descriptions of the sections, the terms anterior and posterior correspond to ventral and dorsal respectively, whilst the terms superior and inferior refer to an upper (cephalic) and lower (caudal) level.

section was made from a cat which lived thirteen days. Comparing the crusta on both sides, the contrast is marked. The degenerate crusta is composed entirely of degenerate nerve fibres stained black by the osmic acid; it is flattened and atrophied, and this atrophy extends to the subject substantia nigra and, in fact, slightly to the whole of the tegmentum of that side. In the opposite crusta there is not one degenerate fibre. There is no degeneration of the fillet, nor, indeed, marked atrophy. The wound is seen to extend towards the grey matter of the aqueduct of Sylvius and to involve the position of the commencement of the descending root of the Vth nerve (E). From about the same region conspicuously degenerate fibres arch round the grey matter, to cross the raphé to the opposite side, where some turn down in the raphé in the position of (C'), whilst others, derived from more anterior decussating fibres, extend forwards and outwards and come to a position (B), behind the inner border of the normal crusta and close to the mesial and dorsal aspect of the lemniscus. These anterior decussating fibres will have in their course passed to the mesial and ventral aspect of the red nucleus, or even partly through the anterior part of the nucleus and of the superior cerebellar peduncle which runs down from it. In fact, the fibres of both tracts must considerably intermingle. This is rendered clearer by comparison with cases in which, owing to the removal of one lobe of the cerebellum, the superior cerebellar peduncle has degenerated upwards to the red nucleus.

The fibres which, having decussated as above and crossed the middle line to the opposite side, have turned down in the raphé (tiefes Mark), in the position of C', fig. 1, that is internal to and slightly behind the red nucleus, and in front of the posterior longitudinal bundle, I will, for the purpose of clearness, call the antero lateral columnar fibres, whilst the fibres B, fig. 1, which are more anterior and lateral, I will term the lateral columnar fibres. Thus two groups of fibres have decussated at this level from the left or injured side.

Occasionally the presence of a very few degenerated fibres on the right side may be demonstrated, passing round the aqueduct to turn down in the raphé of the opposite side, as antero-lateral columnar fibres of the left side. Their number appears to depend entirely upon the extent of the lesion posteriorly into the roof of the aqueduct.

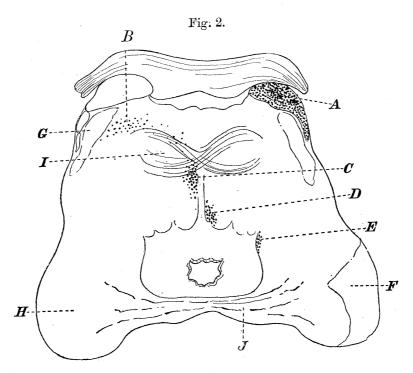
Although fig. 1 shows that on the left side the decussating fibres appear to arise in a focus which coincides with the commencement of the descending root of the Vth, yet an examination of many sections will show that some of the fibres originate further out in the tegmentum.

In the roof of the aqueduct there is a considerable number of degenerate commisural fibres; they appear to terminate in the posterior quadrigeminal body of the sound side. Owing, however, to their very short length and close proximity to the wound, the direction of the degeneration cannot be determined in these sections (see later).

Comparing the posterior longitudinal bundles, it will be seen that there is a well-defined group of small degenerate fibres in the posterior longitudinal bundle of the

left side (side of lesion). As seen in fig. 1, the fibres are close to the middle line and the grey matter of the floor of the aqueduct; they would lie, therefore, at a slightly higher level, in close relationship with the nucleus of the IIIrd nerve. The presence of these degenerated fibres is one of the most constant phenomena in this series of ablation experiments; and it does not appear to depend upon the extension of the wound to the middle line at the level of the IIIrd nerve.

Upper Border of Pons.—Descending from the preceding level, a very short distance, to the upper border of the pons, at the level depicted in figs. 2 and 3, it is

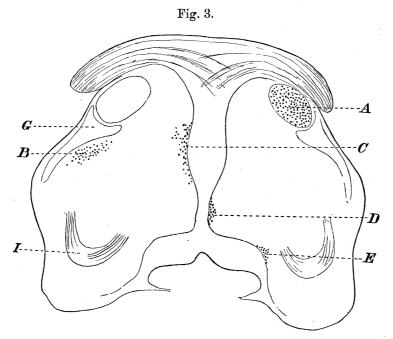


Transverse section passing through the upper (cephalic) border of pons and the posterior corpora quadrigemina. A, B, C, D, E, F, G, as in fig. 1; J, degenerate commissural fibres in the roof of the aqueduct; I, superior cerebellar decussation.

seen that the pyramids have approached one another, each lemniscus appearing in consequence to have passed slightly outwards and backwards. The mesial portion of the tegmentum is occupied by the decussation of the superior cerebellar peduncles, fig. 2, and between these decussating fibres and the dorsal aspect of the pyramidal fibres lie the collection of the lateral columnar fibres upon the right side. At a very slightly lower level, fig. 3, the decussation of the peduncles having been completed, the lateral longitudinal fibres have a slightly more lateral situation, beneath the fillet, from which they are quite distinct.

The antero-lateral columnar fibres on the right side are well seen along the raphé, extending from the anterior border of the posterior longitudinal bundle, slightly into the superior cerebellar peduncle. The majority of the degenerate fibres are massed

close in front of the posterior longitudinal bundle; but scattered fibres extend forwards for about one-half to two-thirds the length of the raphé, figs. 2 and 3. Upon the left side is the degenerate pyramid beginning to break up into separate bundles. The degenerate fibres in the dorsal part of the posterior longitudinal bundle are well seen, also more anteriorly a few scattered fibres in the anterior columnar group. At a slightly lower level some of the degenerate fibres in the posterior longitudinal bundle have moved forwards. Upon the same side the degenerate descending root of the Vth is conspicuous, figs. 2 and 3. A few degenerate fibres may be encountered upon the left side in the position of the lateral longitudinal fibres. They are very often completely absent, but in two cases they have been as conspicuous as those on



Transverse section through upper (cephalic) margin of pons and caudal extremities of post. corp. quad. A, B, C, D, E, G, as before; I, superior cerebellar peduncle.

the right side. The variation depends entirely upon the extension of the wound mesially and downwards in the region of the mesencephalon. If the wound is extensive and penetrates low down, then both the lateral columnar fibres and anterolateral columnar fibres of the left side are interrupted in their course and, in consequence, degenerate.

Apart from the groups of degenerate fibres described above, it is extremely rare to encounter scattered degenerate fibres.

Pons at Level of Vth Nerve.—The pyramids have, at this level, broken up into bundles, and these on the left side are completely degenerate, whilst on the right there are no degenerate fibres.

The most posterior of the degenerate antero-lateral columnar fibres of the right

side have moved slightly forwards, and the same is the case with the degenerate fibres in the *posterior longitudinal bundle* and the two or three scattered degenerate fibres in front of them. This gradual moving forward of the fibres is very characteristic and extends into the cord, but the relative position of the two groups of fibres is constant—those on the right side (anterior columnar fibres) are *always* more in advance of those on the left side (posterior longitudinal fibres).

On both sides the descending root of the Vth nerve can be clearly seen as it passes out from the lateral angle of the floor of the fourth ventricle to gain the anterior and inner part of the rest of the Vth nerve, fig. 4, E. In its course the root descends loops downwards, coming into contact with the VIIth nerve, and then ascends slightly to its exit. Depending upon the direction of the section, the degenerate fibres may be seen issuing in a bundle, or, owing to the looping, the root may be cut twice, viz., as it is descending and ascending. There are no degenerate fibres in the opposite Vth.

It would seem therefore that the degenerate descending fibres of the Vth sweep out, without a junction into the motor root, just as the ascending fibres of the Vth sweep in from the sensory root and degenerate downwards in the ascending root.

But not all the fibres in the descending trunk of the Vth are at the lower levels degenerate; there is an accession of new fibres from the grey matter at lower levels.

The lateral columnar fibres on the right side are recognized as a well marked degenerate group, situated just in front of the motor root of the Vth. They have thus assumed a more dorsal position, as compared with higher levels, but the change is gradual and the difference of position not very great; from this level to the lateral column of the cord, their relative position remains the same.

In the same position on the *left* side, two or three scattered fibres or a well marked bundle may be found, depending, as above stated, upon the extent of the lesion.

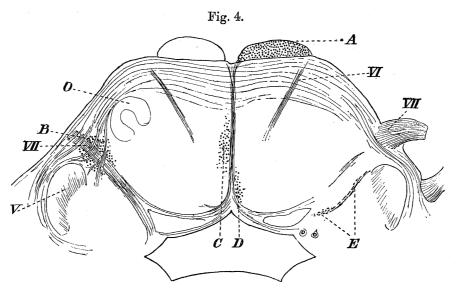
Level of VIIth and VIIIth Nerves. Fig. 4.—At this level the thick VIIth nerve is readily recognized passing outwards from the grey matter of the floor of the fourth ventricle, the VIIIth nerve is close behind separated by the conspicuous and just entering ascending root of the Vth. The commencement of the olive, of the nucleus lateralis, and of the substantia gelatinosa may be observed.

The anterior columnar fibres and the posterior longitudinal bundle have much the same position.

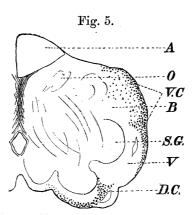
The lateral columnar fibres lie near the point of exit of the VIIth nerve, the latter nerve passing through them posteriorly, fig. 4; they are also traversed by trapezoid fibres. They lie just in front of the descending root of the Vth and of the substantia gelatinosa on the inner side of this; in front and slightly towards the middle line is the commencing nucleus lateralis. At E, the descending root of the Vth has nearly all passed out, below this level it is not seen.

Through the Medulla.—The pyramids lie close together, the degenerate slightly atrophied one contrasting well with its fellow. The antero-lateral columnar and

posterior longitudinal fibres, fig. 1, Plate 3, stand out well, the former in advance of the latter. It will be readily seen from the figure that the relative number of degenerate fibres in the posterior longitudinal bundle is very small. The anterior columnar fibres do not encroach upon the interolivary layer of fibres.



Transverse section through the lower (caudal) end of the pons. A, B, C, D, as before; E, exit of the descending root of the Vth; O, olive.



Section through the lower (caudal) end of the medulla, from a cat in which a hemisection was made in the lower cervical spinal cord. A, pyramid; B, area of the lateral columnar bundle in front of the sub-gelatinosa and to the inside of the cerebellar tracts; V, ascending root of the Vth; V.C, dorsal and ventral cerebellar tracts; D.C, degenerate ascending fibres from the posterior column.

The lateral columnar fibres have the same position in front of the substantial gelatinosa and behind the nucleus lateralis (reticularis). Compared with a section made very nearly at the same level, fig. 5, and representing an ascending degeneration, following upon hemisection of the cord in the cervical region, it will be seen conclusively that the area of the lateral columnar fibres is not encroached upon to

any extent by either the lateral or anterior cerebellar tracts; the fibres of the latter tracts are separated for the most part by the nucleus lateralis and a slight backward projection from it (? nucleus of lateral cerebellar tract).

Level of Decussation of Pyramids.—At this level a reduction in area has taken place.

This is owing to the disappearance of grey matter; the nuclei of the columns of Goll and Burdach are mere projections, the substantia gelatinosa is reduced. The large nucleus lateralis has nearly completely gone, being now represented as the lateral cornu of the anterior horn, which has begun to appear at this level. The nucleus lateralis, therefore, does not represent the anterior horn, which is formed independently.

With the disappearance of the nucleus lateralis, and of the smaller collection of grey matter which may represent the nucleus of the lateral cerebellar tract, the lateral and anterior columns of the cord are formed, and occupy the area extending from the substantia gelatinosa, around the lateral, anterior, and inner aspects of the anterior horn, to the anterior commissure. There has been a great addition of white fibres, and the relative positions of the degenerate lateral and anterior columnar and posterior longitudinal fibres show this very strikingly.

In the right side, the degenerate *lateral columnar* fibres are seen exactly in the position they had higher up, namely, in front of the substantia gelatinosa; on their outer side are the fibres of the lateral cerebellar tract.

The anterior columnar fibres on the right side are seen in the anterior column close up to the pyramidal fibres, fig. 3, Plate 3, occupying the anterior portion of the anterior column and extending slightly into the antero-lateral column. They have much the same position they had higher up, fig. 1, Plate 3; but, owing to the change of position of the pyramids, instead of lying behind the latter, they lie now on their outer aspect, in contact with them. On the left side the degenerate fibres of the posterior longitudinal bundle are also readily recognized in the anterior column, more posterior, as usual, than the degenerate fibres on the opposite side, but like them close up to the pyramid.

The pyramids having sunk deeply into the anterior median fissure to a point close in front of the central canal (fig. 3, Plate 3), commence to decussate. The degenerate pyramidal fibres of the left side are conspicuous. They are seen to cross in bundles the anterior cornu, and to occupy a position very closely posterior to the degenerate lateral columnar fibres, this position being allowed by the attenuation of the substantia gelatinosa. At a little lower level the complete decussation may be observed, none of the fibres being apparently left behind in the anterior column, but a few curve round to the crossed tract on the same side.

There are, therefore, on the right side, in the spinal cord—

- 1. The crossed pyramidal tract.
- 2. The lateral longitudinal fibres in front, and partly mixing with them.

3. The antero-lateral longitudinal fibres.

On the left side—

- 1. A few pyramidal fibres in the lateral pyramidal tract (direct lateral pyramidal tract).
- 2. The lateral longitudinal fibres, when these have been injured on that side, as explained in the text.
 - 3. The fibres of the posterior longitudinal bundle.

There are no direct anterior pyramidal tracts.

We have now traced direct fibres from the level of the posterior corpora quadrigemina into the anterior and lateral columns of the cord, and we have justified the use of the terms anterior and lateral columnar fibres. We have likewise shown that fibres of the posterior longitudinal bundle also descend from the same level into the anterior column.

The gradual passage forward of the anterior columnar fibres as well as the fibres of the posterior longitudinal bundle will have been noted, indicating, therefore, that new fibres have been coming into these tracts. As the level of the decussation is approached fibres increase rapidly, and just below the decussation the anterior and lateral columns have greatly swollen out. It is also to be observed that not all the fibres of the posterior longitudinal bundle, nor of the anterior and lateral columnar systems, at even the highest levels, are degenerate.

Cervical, Dorsal, and Lumbar Cord.—After the pyramids have left the anterior columns, the degenerate anterior columnar and posterior longitudinal fibres stand boldly out, and might be readily mistaken for direct pyramidal fibres; indeed, I at first mistook them for them. As one descends the cervical region, both sets of fibres tend to move away from the inner edge of the anterior column; this is due to the insertion of new fibres, a circumstance which is worthy of note in connection with the question of the so-called direct pyramidal tract. Both sets of fibres at the same time grow less, and have disappeared in the upper dorsal or lower cervical region.

In the posterior portion of the lateral column, the characteristic small degenerate fibres of the crossed pyramidal tracts are readily distinguished; in front of them is a triangular area of much larger degenerate fibres—the lateral columnar fibres. The two together form a pyramidal-shaped area of degeneration (fig. 4, Plate 3), which most observers would hold to be typical of the crossed tract. Yet, as we have seen, the origin of the two is very distinct. In fig. 5, Plate 3, which represents the left side, and where there is no degenerate pyramid, but degenerate lateral columnar fibres, which we could readily trace from the mesencephalon, the differentiation of the two tracts is very clear, both as regards topography and the size of the fibres. It will be seen the cerebellar tracts are not encroached upon to any extent—a point which is further emphasized by comparison with an ascending degeneration in the region in question. The lateral cerebellar tract and the hinder part of the anterior cerebellar tract fairly accurately outline a slightly bilobed area occupied by both

descending tracts. Traced towards the lumbar region, both sets of fibres diminish, but the lateral columnar thin out first.

We have stated that on the normal or right side, in the mesencephalon, pons and medulla there were no degenerate fibres in the pyramidal tract; and this seems also to obtain in cases after the tract has decussated in the cord. But I have seen a few fibres of the degenerated pyramid decussating over to their own side to run down in the lateral pyramid of that side. I again at first used this observation to explain the presence of the degenerate lateral columnar fibres on the left side, in apparently the position of the crossed pyramidal tract. We will return to these points in the general discussion.

The Degenerations Resulting from Removal of the Motor Area in the Cat.

The material furnished by four cats which had recovered well after the abovenamed operation furnished the basis of this investigation.

Description of Operation.—With the same precautions as in the preceding ex periments, the anterior portion of the brain was removed with bistoury and scoop, so as to ensure the complete removal of the motor zone.

Anatomical Changes.—Reserving the paths of degeneration in the brain for a subsequent chapter, a section through the mesencephalon at the level of the posterior corpora quadrigemina, showed striking degeneration and slight atrophy of the crusta, in fact, the same as in the case of the removal of the hemisphere. There were, apart from the crusta and a few fibres in the roof of the aqueduct, no other signs of degeneration. The IIIrd nerves, the descending root of the Vth, the anterior and lateral columnar fibres, and the posterior longitudinal bundles were absolutely intact.

Fig. 2, Plate 3, represents a section through the *medulla*, and the only degenerate fibres present were those in the pyramid; the comparison with the hemisphere cats is striking, fig. 1, Plate 3.

In the *cervical cord* there are no degenerate fibres in the anterior columns. In the lateral column the round bundle formed by the small degenerate fibres of the crossed pyramidal tract, fig. 6, Plate 3, are well seen, but there are no scattered *large* fibres belonging to the lateral columnar system.

The contrast therefore between removal of a whole hemisphere and the anterior motor part only, is complete, and argues strongly for the accuracy of the results.

The degeneration in the crossed pyramidal tract can be followed into the lumbar region.

The Degenerations Resulting from Hemisection of the Cervical Spinal Cord.

The spinal cords of four cats were investigated.

The hemisection was made on the right side, in the usual way and with the greatest

If this is not done, complete transverse myelitis occurs, with the production of very many anomalous paths of degeneration. The hemisection was made a short distance below the decussation. When a section is examined through the cervical cord a short distance below the lesion, it is seen that the lesion is confined to one In the degenerate half the changes are well known to differ from those obtaining in lesions of the motor area. The comparisons are, however, most important. The Γ -shaped degeneration in the anterior column is very noticeable, it tapers away antero-laterally, but along the inner half of the anterior column it forms a distinct tract, a tract, moreover, which, without any staining reaction, may be readily recognized by the size of its fibres. The figures show that a small area along the inner margin of the anterior column remains free from degeneration, whilst at lower levels the degenerate fibres recede still further from the median fissure and at the same time rapidly diminish. I have as yet had no evidence to show that there are ascending fibres along the inner margins of the anterior columns, as described by SHERRINGTON and MOTT; but I have not examined the point particularly, as it is outside the scope of the present work.

Next to the antero-lateral tract degeneration, the most striking degeneration is in the region of the crossed pyramidal tract. The degeneration at this spot has the pyramidal or bilobed character which was described above after the removal of one hemisphere. The more rounded posterior portion consists not only of the small fibres characteristic of the pyramid, but also of larger ones; the anterior portion is made up of the larger fibres. In the lower dorsal region, fig. 36, the pyramidal area is actually separated into two parts, one a posterior rounded portion, and the other a more scattered marginal part. From our previous knowledge we may be perhaps right in saying that the rounded posterior part corresponds in the main to the crossed pyramidal tract, but also contains other large fibres which have entered it; whilst the anterior, marginal scattered fibres represent lateral columnar fibres. In addition to the larger tracts, there are numerous degenerate fibres scattered throughout the lateral and antero-lateral columns. Compared with an ascending degeneration, it will be seen that, with the exception of Gowers' tract, there is not much intermingling of fibres.

Close to the seat of the hemisection many degenerate fibres may be observed crossing over to the opposite side, some passing through the grey matter, others in the anterior commissure. Corresponding to this I have observed many degenerate fibres in the anterior column close to the grey matter of the anterior horn, at a short distance below the seat of lesion; at still lower levels fibres may be seen in the lateral column. The scattered degenerate fibres are larger, and it seems very unlikely that any of them are derived from the degenerate pyramidal tract of the opposite side, that is, that they are "re-crossed" fibres.

The Degenerations resulting from Removal of a Lateral Lobe of the Cerebellum.

These degenerations I have not thoroughly examined, as my colleague, Dr. Russell, is engaged upon this task. But I can state that what I have found so far in the cat agrees with our present anatomical knowledge, and does not coincide with the extensive changes described and figured by Marchi.

I have always obtained degeneration of the superior cerebellar peduncle.

In the same cats there was no degeneration in the posterior longitudinal bundle, in the antero-lateral columnar fibres or in the lateral columnar fibres.

The Degenerations resulting from Division of the Crus Cerebri.

In the two cats, whose symptoms are described further on, and which were kept alive for 5 weeks, the degenerative changes were precisely similar to those seen in the hemisphere cats. The wound was sharply differentiated and strictly bilateral; in both cases there was complete degeneration of the crusta on the side of the lesion. The other degenerations were as follows:—

On same side—

- 1. Descending root of Vth.
- 2. Posterior longitudinal bundle, mesial aspect of (not complete).

On opposite side—

- 1. Antero-lateral columnar bundle.
- 2. Lateral columnar bundle.

The usual tracts were traced into the cord; there were traces of a direct lateral pyramidal tract; the crossed pyramidal tract ended about the mid-lumbar region.

The Degenerations found in the Brain after (1) Removal of One Hemisphere, (2) Removal of the Anterior Portion of the Brain, (3) Division of the Crus Cerebri.

Removal of One Hemisphere.—The chief degeneration was limited to the corpus callosum, the degeneration extending its whole length, but more marked anteriorly just in front of its centre, and again posteriorly near the splenium.

With a view of ascertaining in what direction the callosal fibres turned, sections were made in an antero-posterior vertical direction, in a lateral vertical direction, and from side to side. It was found that the degenerate fibres radiated for the most part upwards, anteriorly, and straight across, but none could be traced into the internal capsule to turn down into the crusta. The fibres of the posterior commissure, as already mentioned, were degenerate, so also the commissural fibres in the pineal body—a tract of fibres described by Darkschewitsch. The optic tract on the left side was usually injured, and showed in consequence widespread degenerations. The anterior commissure was not degenerate.

Removal of Anterior Area of Brain.—The degeneration in the corpus callosum can be very well seen; it is most marked anteriorly, and again near the posterior extremity. No fibres whatever turn down into the internal capsule to reach the crusta.

In vertical transverse sections it was not easy to follow the radiating degenerate callosal fibres; the anterior median group appeared to pass out anteriorly, but what becomes of the more posterior fibres I am unable at present to say.

There was atrophy of the *subcallosal layer* of Muratoff on the side of the lesion, but, contrary to Muratoff, I only observed a few scattered degenerate fibres in it.

A very large area of the internal capsule, in vertical transverse sections, showed degeneration, the lowermost portion, and groups of nerve-fibres on its inner aspect, however, contained no degenerate fibres. Slightly behind the level of the optic chiasma, in similarly made sections, degenerate fibres were traced from the capsule entering the thalamus, where they collected and grouped themselves around the lower and inner aspect of the ventral lateral geniculate body. In more posteriorlymade sections they have passed forward beneath the pulvinar; then, with the disppearance of the geniculate bodies and pulvinar, the fibres came to the surface as a well-marked group, immediately external to the commencing anterior corpus quadrigeminum; they are not connected with the other fibres at this level, which are going to the posterior commissure. In sections through the anterior corpora quadrigemina, the degenerate fibres are seen to enter the base of the corpus of the side of the lesion; and it would seem probable that some fibres terminate here. Other fibres, however, keep on their oblique course, and cross over superficially in the roof of the aqueduct to the opposite side, where they may possibly terminate in either of the corpora quadrigemina. If the above observations should always turn out constant, and they have done so in the two cases examined, it would show that the anterior third of the brain, and possibly of this, the motor region, was in communication with both halves of the important quadrigeminal region.

These are not, however, the only fibres observed from the capsule which pass to the quadrigeminal region; fibres can be traced in successive sections back to the quadrigeminal region, which are being given off from the degenerate fibres in the normal capsule in their course to form the crusta. One well-marked bundle passes from the upper and incurved extremity of the pyramid just before the crusta is formed, to the roof of the aqueduct, and lower down isolated fibres come off from the corresponding extremity of the crusta (outer and upper extremity) and curve round to the quadrigeminal region; these latter fibres are figured by Muratoff.

Discussion of the Preceding Anatomical Facts and of the Literature relating to them.

In the preceding pages we have traced from the vicinity of the corpora quadrigemina, certain definite groups of degenerate nerve fibres, viz., the descending root

of the Vth fibres in the posterior longitudinal bundle, and fibres which we named anterior and lateral columnar fibres. In the grey matter of the floor of the aqueduct are the important nuclei of the IIIrd nerves, and further out in the tegmentum the large red nuclei. From the superior corpora quadrigemina fibres are said to pass to the cortex and optic tract.* The region is thus the meeting point of fibres related to the cord, cortex, cerebellum, the olives, the optic, and certain other very important nerves.

Posterior Longitudinal Bundle.—In Edinger's† words: "Das tiefe Mark ist ein phylogenetisch sehr altes System. Es fehlt selbst in den einfachst gebauten Gehirnen niederer Wirbelthiere nicht, und umgiebt sich bei diesen, wie auch beim Menschen, ausserordentlich frühzeitig mit Markscheiden."

At the ninth month, according to the same authority, the fibres of the posterior longitudinal bundle, and those of the fasciculus retroflexus, are medullated. Dark-SCHEWITSCH showed that in the 28 centims. long feetus the ventral portion of the posterior commissure is already medullated, and maintains that fibres arch from this portion of the commissure around the grey matter of the aqueduct and come into relationship with the upper oculomotor nucleus and the posterior longitudinal bundle. Both Edinger and Darkschewitsch state that the posterior longitudinal bundle receives large accessions of fibres from the posterior commissure and the oculomotor nucleus, and that other fibres have an origin higher up in the brain. From the change in position of the degenerate fibres in the same bundle at lower levels, as described in the preceding pages, it is most probable that new fibres are being continually added to this system. Spitzka, as the result of a lesion in the left cerebral peduncle in the cat, describes atrophy of the left posterior longitudinal bundle, and associates it with the atrophy of the left anterior corpus quadrigeminum which was present. He combats the view that the posterior longitudinal bundle has an origin in the lenticular nucleus or in the cortex, as Meynert, and to a certain extent, Wernicke assert; and in additional support of this he brings forward his well-known observations of the large size in reptiles where the anterior corpora quadrigemina are large. He further states that in atrophy, limited to the hemisphere, there is no change in the bundle. According to Forel the posterior longitudinal bundle is very small in the mole; Gudden, on the other hand, states that although in the same animal the nuclei of the IIIrd nerves are atrophied, yet the posterior longitudinal bundle is of fair size.

- * 'Neurolog. Centralblatt,' 1885.
- † Edinger, 'Nervöse Centralorgane.' Leipzig, 1892.
- ‡ Edinger states that the fibres are medullated between 6th and 7th months, but that they are not all medullated at same time.
 - § Darkschewitsch, "Ueber die hintere Commissur des Gehirns," 'Neurolog. Centralblatt, 1885.
- || Spitzka, "Degenerations resulting from lesions of the thalamus and neighbouring part of the cerebral peduncle in cat," 'Neurolog. Centralblatt,' 1885; also "Architecture and Mechanism of the Brain." 'Chicago Journ. of Nerve and Mental Diseases,' 1879.

SPITZKA (l.c.) makes the remark that the posterior longitudinal bundle connects the higher centres in the anterior corpora quadrigemina with the nuclei of the movements of the eyes, and those of the turning of the head; Flechsig, that it is a connection both between the IIIrd, IVth, and VIth nerves, and perhaps other nerves. Obersteiner* concludes "that the posterior longitudinal bundles consist for the most part of short fibres connecting together the motor nuclei which follow one another from the spinal cord up to the brain."

Bruce[†] figures the tract of various dimensions at different levels and describes fibres entering it from the opposite side of the raphé. Numerous cranial nerves, according to the same authority, give or receive fibres from it.

BECHTEREW‡ describes the projection into the "inner area" of the formatio reticularis (Flechsic) of the anterior columnar ground bundle, and of part of the lateral columnar ground bundle, and says that the former constitutes the posterior longitudinal bundle; they, however, end at some little distance above the medulla and their place is taken by oculo-motor fibres.

Reviewing the literature upon cortical extirpation, there is no mention of degeneration or atrophy of the posterior longitudinal bundle, and apart from Spitzka's observation (l.c.) of its atrophy in a case of lesion of the quadrigeminal area, I have not been able to find any experimental reference to it. There is likewise very little recorded from the side of pathology. In cases of porencephaly its presence is normal. Jakowenko\sqrt{ecords} a case of degeneration of both bundles in man; but he does not appear to have traced them very completely. He states that they may contain short fibres which bind the various centres, and long ones, sensory, which show an ascending degeneration. Finally Marchi after extirpation of one half of the cerebellum, appears to obtain widespread degeneration of the posterior longitudinal bundle both above and below the lesion. This surely cannot imply that all the fibres of the posterior longitudinal bundle are derived from the cerebellum, for there is no anatomical support for such a belief.

In the cat the fibres which form the posterior longitudinal bundle begin to group themselves a short distance above the level of the root of the oculo-motor nerve, but although bounded posteriorly by the grey matter of the aqueduct, externally it would be impossible to separate them from other descending fibres in the recticular formation of the tegmentum at this level. At a still slightly higher level, that is immediately ventral to the posterior commissure and pineal body, portion of what is apparently the fasciculus retroflexus occupies the space in front and to the outside of the grey

- * OBERSTEINER, 'The Anatomy of the Central Nervous Organs,' trs. Hill, 1890.
- † Bruce, 'Illustrations of the Mid and Hind Brain,' Edin., 1892.
- ‡ Becterew, "Ueber die Langsfaserzüge des Formatio-reticularis medullæ oblongatæ et pontis." 'Neurolog. Centrlblatt,' 1885.
- § Jakowenko, "Zur Frage über den Bau des hintern Längsbündels (fasciculus longitudinalis posterior)." Ref. 'Neurolog. Centralblatt,' 1888.

matter of the aqueduct, the fibres of what will be the posterior longitudinal bundle lying dorsal to them. This brings the longitudinal fibres therefore very close to the posterior commissure, but it is very difficult to see how the fibres of the latter, which are transverse, can suddenly turn and become longitudinal. I cannot prove to myself that the fibres of the posterior commissure, which are constantly degenerate in my preparation are the degenerate fibres which I have shown to be present in the posterior longitudinal bundle. DARKSCHEWITSCH* on the other hand, however, tries to show that fibres of the ventral portion of the commissure do turn sharply into the upper oculo-motor nucleus and into the space between the fasciculus retroflexus and red nucleus and the grey matter of the aqueduct to become longitudinal fibres. At this region in horizontal sections, one can see in my preparations, degenerate fibres (which certainly, I admit, might be derived from the degenerate fibres of the posterior commissure), pass caudally into the position of the posterior longitudinal bundle. I am, however, much more inclined to the belief that the degenerate fibres in the posterior longitudinal bundle arise on the same side from the nucleus of the posterior longitudinal bundles (EDINGER, fig. 69), which may be regarded as the highest portion of the anterior sylvian grey matter. In transverse sections, just below the fasciculus retroflexus, but still above the root of the IIIrd nerve, the same degenerate fibres can be seen, cut obliquely, next to the grey matter of the aqueduct, passing from the position of the upper oculo-motor nucleus down near the anterior extremity of the grey matter. These appearances therefore correspond in a remarkable degree with the figure 1 of the human feetus in Darkschewitsch's paper; but the degenerate fibres are, after all, only a few, and they appear, in their course just described, to insinuate themselves between the grey matter of the aqueduct and the larger body of normal fibres, which lie dorsal and external to the fasciculus retroflexus (see above), and appear to go to form the main mass of the posterior longitudinal bundle. What the origin of these undegenerate fibres may be I cannot state definitely; there is much in favour of the view that they arise from or in the neighbourhood of the above-mentioned nucleus.

At the level of the root of the IIIrd nerve, the degenerate fibres come into close contact with the large oculomotor nucleus and with the fibres issuing from it; just below the root, they are readily seen grouped together, occupying the most posterior position of the fibres in the bundle, viz., against the grey matter.

Since the IIIrd nerve was so frequently degenerate in the hemisphere cats, on the side of the lesion, I at one time thought, that possibly the degenerate fibres in the IIIrd nerve might turn down and form the degenerate fibres in the posterior longitudinal bundle, or that the latter might arise from the oculo-motor nucleus. This cannot be their source, for as just mentioned degenerate fibres are encountered at higher levels. Nor is there evidence to show that any of the descending fibres,

^{*} Darkschewitsch, "Einige Bemerkungen über Faserverlauf in der hinteren Commissur des Gehirns," 'Neurolog. Centralblatt,' 1886.

from the posterior commissure, run out into the IIIrd nerve. To sum up, the possible sources of the degenerate fibres which presented themselves to me are:

1. The highest portion of the sylvian grey matter (the nucleus of the posterior longitudinal bundle); 2, the posterior commissure; 3, the superior and the inferior oculo-motor nuclei; 4, the oculo-motor nerve; 5, the thalamus; 6, the internal capsule. The first appears the more probable view. Evidence therefore tends to show, owing to the few fibres which are degenerate, that the fibres of the posterior longitudinal bundle are mixed at this high level; but I am not so sure that the bundle receives a large addition of fibres from the nucleus of the IIIrd nerve, as usually stated. Finally it may be observed in this place, that Darkschewitsch speaks of the fibres as ascending into the posterior commissure, whilst my fibres degenerate downwards.

Just below the level of the IIIrd nerve, fig. 1, not only is the group of degenerate fibres well-marked, but also the whole posterior longitudinal bundle. They are bounded in front by the degenerate decussating fibres.

Although the degenerate fibres can apparently be traced from the level of the posterior commissure to the cervical region, it is possible that some become connected with the nuclei of the different nerves, but the method employed furnishes no proof of it.

It is worthy of note that as the posterior longitudinal bundle enters the anterior column of the cord, the degenerate fibres occupy their usual internal position; we may therefore assume that the other fibres of the bundle are those occupying the zone next the grey matter. In the cord, after hemisections, it is the internal fibres which degenerate down for long distances, whilst those in the zone, next the grey matter, are short fibres. It is very likely, therefore, that the same process is continued upwards, and that our degenerate fibres are homologous to long internuncial fibres, whilst the non-degenerate ones correspond to short fibres. The similarity is certainly striking, both from the point of view of position, of direction of degeneration, and of non-decussation.

The Antero-lateral Columnar Fibres.—The degenerate fibres which are so clearly seen in fig. 1, Plate 3, passing from about the position of the descending root of the Vth and crossing the raphé immediately in front of the posterior longitudinal bundle, represent the fountain-like decussation of Meynert. The same fibres are well seen in fig. 78 of Edinger's "Vorlesungen," 1892, internal to the fasciculus, retroflexus, and red-nucleus, but they are supposed to end soon in nerve cells in this position. According to the same authority the fibres are strongly marked in fishes and birds.

In fig. 1, they are represented at a level just below the exit of the IIIrd nerves, and are encountered in transverse sections from the level of the IIIrd nerves to a short distance below. In sagittal section they appear to extend from the level of the hinder part of the anterior corpus quadrigeminum to beneath the posterior corpus.

It is exceedingly difficult to make absolutely sure of their origin. I am unable, so

far, to trace them definitely to either the posterior commissure or the commissural fibres behind these in the roof of the aqueduct. The impression is rather given that they spring from the lateral area of the grey matter of the aqueduct, from indeed the area closely related to the descending root of the Vth, from the cells in which Meyner believed they originated, and from which circumstance he named them "Quintus-stränge." Instead of the fibres ending in nerve cells in the inter-red-nuclear region, we have rendered it clear that they pass down through the pons and medulla into the cord, and that they form in their course an exceedingly characteristic group, in front of the posterior longitudinal bundle.

Above the nucleus centralis inferior I can find no special reference to these fibres; little attention has been given apparently to the higher regions of the reticular formation which lies between the post longitudinal bundle and the fillet; fibres have been described decussating in it and becoming longitudinal, but long fibres, unless indeed they are described and included in either the posterior longitudinal bundle or fillet, have not, in so far as I am aware, been discussed. A glance at the figures in Plate 3 will show that these anterior columnar fibres are not included in the lemniscus as the latter is usually figured and understood. In the lesion through the crus, the lemniscus will have been often divided, but there is no descending degeneration in it, whilst the anterior columnar fibres are markedly degenerate. Lower down, however, in the medulla for example, fibres of the anterior column are described mixing with the interolivary fillet. Thus, in tracing the upward continuation of antero-lateral columns of the cord, the anterior is said to be represented by the posterior longitudinal bundle, whilst fibres derived from the lateral tract occupy the position in front of the latter and behind the commencing fillet (OBERSTEINER), that is that the antero-lateral tracts (excluding the ascending tracts) move inwards to a mesial position. Bechterew,* in a paper upon the constitution of the reticular formation in the medulla and pons, based upon the study of the 25 to 28 centims. long fœtus, concludes that all the fibres of the anterior columnar ground bundle as well as the anterior portion of the lateral columnar ground bundle, pass into the inner area of the formatio reticularis. He states that at the level of the middle of the lower olive, the medial raphé fibres are grouped into two bundles; the dorsal group are the posterior longitudinal bundles, and are composed exclusively of the upward projection of the anterior columnar ground bundle; the ventral bundle which extends to the interclivary layer, and which is less compact, is composed of fibres of the lateral columnar ground bundle. Traced higher, the fibres of the anterior group end in the nucleus centralis of Roller. He, however, states that fibres, anterior and external to the posterior longitudinal bundle, and which perhaps arise from the anterior columnar ground bundle, can be traced still higher to the reticular nucleus in the pons, together with fibres corresponding to anterior columnar ground bundle fibres,

^{*} Bechterew, "Ueber die Langfaserzüge der Formatio reticularis medullæ oblongatæ et pontis," 'Neurol. Centralblatt,' 1885.

but which have been broken in the central nucleus; a little higher up, at the level of the nucleus centralis superior, all the fibres in front of the posterior longitudinal bundle, which might correspond to the anterior columnar ground bundle, have disappeared. According to my showing, in the cat fibres of the antero lateral column of the cord, can be traced without interruption to Meynerr's decussating fibres. Traced into the cord, as mentioned in the preceding pages, the columnar fibres pass into the anterior column and into the area in front of the anterior cornu. They lie in front of the fibres derived from the posterior longitudinal bundle and extend round the horn; they correspond, therefore, to antero-lateral fibres. It will thus be seen that the results obtained by the Marchi method, as regards the upward projection of the anterior column (posterior longitudinal bundle fibres) and of the antero lateral column coincide with the teaching of embryology and anatomy. They simply extend the latter, by showing that in the cat at least unbroken fibres may be traced from the quadrigeminal region to the cord. They show that the degenerate fibres in the posterior longitudinal bundle continue on the same side as the lesion, whilst the antero-lateral columnar fibres situated on the opposite side have crossed over in MEYNERT'S decussation.

[Since writing the above, I have read a paper by Held* from Flechsig's Laboratory. His description of the origin and destiny of Meynert's fibres nearly accords with mine. He describes Meynert's fibres originating in the upper corpus quadrigeminum, and crossing over in the fountain decussation to take part in the formation of the antero lateral column. In the cat they are very conspicuous on the ventral aspect of the posterior longitudinal bundles; but in man, owing to the development of the superior cerebellar decussation, are pushed to one side. The fibres are the axis cylinder processes of the multipolar ganglia cells, which are chiefly situated in the middle and deep portion of the grey matter of the upper corpus. Some of the fibres he describes, giving collaterals to the oculo-motor nucleus on the same side, then crossing and giving collaterals to the opposite nucleus of the abducens. He states that, as the posterior longitudinal bundle is continued into the anterior column of the cord, it is probable that fibres coming from the ganglion cells of the corpus may extend into the cord, and surmises a further union of the above-mentioned nuclei with the centres in the upper cervical cord for the turning of the head (compare SPITZKA).

He describes fibres originating in the red nucleus which pass down to form the lateral column. These are the fibres which correspond, in all probability, to my lateral columnar fibres, and which my evidence shows arise from cells in the grey matter, more ventrally placed than the cells giving origin to the fibres of the anterolateral columns; but, like the former, they decussate.

A great deal has been written upon the degenerations of the fillet†—some observers

^{*} Held, 'Archiv für Anatomie u. Physiologie,' 1892.

[†] Mahaim, 'Archiv für Psychiat.,' vol. 25; Mott, 'Journal of Physiology,' vol. 15, No. 6.

maintaining that the degeneration is descending, an equal number that it is ascending. It is possible that some of the instances of descending degeneration may be explained by the presence of the antero-lateral columnar fibres. Schrader* describes, in a case in which there was a large lesion in the left crus, descending degeneration of the left median fillet and of external dorso-lateral fibres (around olive). He described the fibres ending in the nuclei of the posterior columns of the opposite side and in the antero lateral column of the same side. Monakow,† in a case in the new-born cat, in which the pons was damaged in removal of a portion of the hemisphere, describes descending degeneration in the inter-olivary fillet. Marchi also figures complete descending degeneration of the fillet, and of the fibres in the raphé and posterior longitudinal bundle, and traces the degeneration into the antero-lateral tract; we have before commented upon the significance of this wide-spread degeneration. Hosel‡ especially lays stress upon a descending atrophy of the "cortical" fillet, which crosses to the grey nuclei of the posterior columns. My own observations lead me to believe that there is no descending degeneration of the fillet.

The Lateral Columnar Fibres.—This system of fibres is closely related to the preceding; they commence in the quadrigeminal region, close in front of the origin of antero-lateral columnar fibres, and are derived from more ventrally decussating fibres. In their course downwards, they separate from the antero lateral columnar fibres and take up a lateral position and pass into the lateral column of the cord. As in the case of the preceding fibres, they have been described by various observers under different names, and have been included in the fillet or the cerebellar tract.

They appear to be derived from fibres which pass from the side of the lesion more ventral to Meynert's fibres, to the opposite side, fig. 1.

It seems probable that these decussating fibres therefore coincide with Forel's decussation. The evidence seems in favour of their being Meynert's fibres, but it is possible that more deeply situate quadrigeminal fibres may take part in their formation. Meynert's described a group of fibres which could be traced into the pons, where they occupied a position between the facial nucleus and the ascending root of the Vth, and were bounded laterally by the corpus trapezoidium. Monakow later described the same fibres in the cat, and termed the group the aberrant lateral columnar bundle. He says that it runs into the cord ventral to the ascending root of the Vth and takes up a position lateral and peripheral to the posterior cornu. Higher up the tract lies between the olive and the outgoing facial, in the position of

^{*} Schrader, 'Ein Grosshirnschenkelherd mit secundären Degenerat. der Pyramide in Haube.' I. D., Halle, 1884. Ref. 'Neurolog. Centralblatt,' 1885.

[†] Monakow, "Neue exper. Beiträge zur Anatomie der Schleife," 'Neurolog. Centralblatt,' 1885.

[‡] Hosel, "Ein weiterer Beitrag zur Lehre vom Verlauf der Rindenschleife," 'Archiv f. Psych.,' vol. 35, Heft 1, 1893.

[§] MEYNERT, 'Archiv für Psychiatrie,' 1884, fig. 52.

[|] Monakow, loc. cit.

N in fig. 123 of Obsteiner's last edition of his "Nervous Anatomy," a position which exactly accords with that figured and described by me in the preceding pages. higher, it is described as entering the fillet, and OBERSTEINER makes the remark that the tract may be identical with the large fibres of the ventral portion of the direct cerebellar tract described by LOEWENTHAL, which do not enter the corpus restiforme, but pass up through the corpus trapezoidium, between the roots of the VIth and VIIth nerves, to near the quadrigeminal region, where it comes in contact with the fillet and the superior cerebellar peduncle and then turns round and enters the cerebellum. The same authority states that, according to Monakow, it is possible that the aberrant bundle goes over in Forel's decussation and ends in the subthalamic region of the opposite side. Bruce describes a lateral medullary tract, lying in front of the direct cerebellar which contains Gower's tract, but is larger; he describes it terminating in the lateral area of the medulla, and "by a special bundle which crosses the corpus trapezoidium, immediately external to the emerging part of the root of the facial nerve, and enters the lateral fillet." Bechterew* describes in the feetus, the hinder part of the lateral columnar ground bundle passing up into the pons in front of the lateral cerebellar tract. He describes the "seitenstrangrest" ending in the nucleus lateralis; he would not, however, deny them continuing unbroken as far as the mesencephalon and cerebrum and emphasises the fact. He says, for instance, that the lateral dorsal system of the formatio, situated dorsal to the nucleus lateralis and to the inner side of the ascending root of the Vth, may be traced upwards in the most external part of the formatio, lying at the lower portion of the pons, external to, and behind the nucleus of the VIIth, in the middle of the pons to the inner side of the motor nucleus of the Vth, and still higher up on the convexity of the superior cerebellar peduncle; here the decussation causes their wide separation, but in the cerebral peduncle they lie again external and behind the red nucleus and may then pass perhaps into the Flechsig's "Haubenstrahlung." The same observer mentions in another paper that the "centrale Haubenbahn" was figured by Stilling in the pons and described as the upward continuation of the lateral column.

The researches of Loewenthal[†] are of special interest from the point of view of the lateral columnar fibres. In an inaugural dissertation, published in 1885, upon the "Dégénérations secondaires de la moelle épinière, consécutives aux lésions expérimentales médullaires et corticales," made in Schiff's laboratory, from the dogs operated on by Schiff, he noticed the presence of large non-degenerate fibres in the degenerate crossed pyramidal tract in dogs after lesion of the cortex, whilst in hemisections in the cervical region there were numerous large non-degenerate fibres in

^{*} Bechterew, "Ueber eine bisher unbekannte Verbindung der grossen Oliven mit dem Grosshirn," 'Neurolog. Centralblatt,' 1885. (Ref. in 'Neurolog. Centralblatt,' 1886.)

[†] LOEWENTHAL, "La région pyramidale de la capsule interne chez le chien et la constitution du cordon antéro-latéral de la moelle," Rev. Méd. de la Suisse Romande, 1886.

the ventral aspect of the degenerate pyramidal tract. They occupied the field between the pyramidal tract and the lateral cerebellar tract, and he looked upon them as a special system of long fibres, and designated them as the outer zone of the lateral column.

In 1886 he extended his observations* upon the dog, and observes that in spite of the removal of the motor area the large fibres between the pyramid and cerebellar tract and those in front of the pyramid and extending marginally are not affected. He tries to show that there exists in the crossed pyramidal tract fibres which are not cortical, that these are most marked in the cervical region, but could be traced to the lumbar; he calls them the "systême intermédiaire." They can be traced upwards with certainty into the medulla outside the formatio-reticularis of Deiters, but they take no share in the pyramidal decussation. On the other hand they have nothing to do with the direct pyramidal tract. He adds that he has not called them "commissural" fibres, as Langley made him state (but this is not the case), but that they might be called the "anterior marginal bundle." In a third paper upon hemisection of the posterior part of the medulla of the kitten, at the level of the decus sation, he mentions especially below the lesion the atrophy of large fibres upon the ventral and external aspect of the pyramid, and which he believes do not belong to the pyramid. In another paper the same conclusions are drawn. Lastly, it may be mentioned that he elsewheret describes ascending degeneration of the lateral cerebellar tract, which, in front of the substantia gelatinosa of the ascending Vth, divides into two, a dorsal and a ventral part, the former passes into the corpus restiforme, the ventral portion, which he assumes is the same as the aberrant lateral columnar tract of Menakow, passes upwards to the neighbourhood of the origin of the Vth, and still further, lying close to the margin of the pons, to near the posterior corpora quadrigemina, where it turns round the superior cerebellar peduncle.

Langley in his "Recent Observations on Degeneration of Nerve Tracts in the Spinal Cord," 'Brain,' 33, makes the remark that Bouchard had in 1866 noticed in man that the descending degeneration in the lateral column was greater after injury to the medulla, than after injury higher up, and that the medullary fibres were situated in the lateral border of the pyramidal tract; he called them the "fibres commissurales antérieures longues." Langley, in discussing the question, agrees with Sherrington that the cortical pyramidal tract is smaller than that given by Flechsig, and proposes the name of descending medullary tract for the other fibres found degenerate in the region of the pyramidal tract after lesions of the medulla.

^{*} LOEWENTHAL, "Atrophies secondaires du cordon postérieur," 'Recueil Zoologique Suisse, 1886.

[†] Herzen et Loewenthal, "Trois cas de lésion médullaire du niveau de jonction de la moelle épinière et du bulbe rachidien," 'Archiv. de Physiologie,' vol. 7, série 3.

[‡] LOEWENTHAL, "Dégénérations secondaires ascendantes dans le bulbe rachidien, dans le pont, et dans l'étage supérieur de l'isthme," 'Rev. Méd. de la Suisse Romande, 1886.

[§] Bouchard, 'Archiv. gén. de Méd.,' 1886.

To sum up, it may be stated that the existence of fibres, following the course indicated above, is not negatived by any anatomical fact. It has been shown that just as in the case of the inner fibres of the posterior longitudinal bundle, and the antero-lateral columnar fibres, there exists a group of unbroken fibres which extend from the quadrigeminal region into the lateral column of the cord. It has been shown that these fibres undergo a descending degeneration, and that they must not be confounded with the fibres of the cerebellar tract, to the inner side of which they The fibres may be traced to the upper lumbar region, but they very greatly diminish as they descend. It will be observed that the fibres are very large, and contrast with the smaller fibres of the crossed pyramidal tract. The fibres are not of cortical original and therefore they cannot explain the cases of bilateral degeneration of the crossed pyramidal tracts following unilateral cortical lesions. essentially non-pyramidal, differing as stated by their position and size. probably the representatives in the medulla, pons, and mesencephalon of the large descending extra-pyramidal fibres found in the lateral columns of the cord, standing in the same relationship to these as do the fibres in the posterior longitudinal bundle and raphé to the anterior and antero-lateral columns. It is possible that in the cat and the dog this higher "internuncial" or segmental system is more marked than in the monkey or in man, just as in the latter examples, the pyramidal system is far more extensive than in the former.

The Pyramidal Tracts.—The fibres of one pyramid alone are found degenerate after removal of the whole motor area or the whole hemisphere; no fibres therefore pass by the corpus callosum, as has been suggested by Hamilton,* into the opposite pyramid. At the decussation the fibres cross to the opposite side, and no direct pyramidal tract is left behind. A few fibres of the pyramid at the lower level of the decussation instead of crossing to the opposite side may curve round in the form of a small bundle to enter the crossed pyramidal tract of its own side. Corresponding with this fact, a very few degenerate fibres may be observed in the crossed pyramidal tract on the same side as the lesion.

Langley,† in summing up the various observations upon descending degenerations, states that in no case apparently did unilateral brain injury cause degeneration of the opposite pyramid, although, in the cord, both crossed tracts might be degenerate. Since then little evidence has been brought forward to show that the opposite pyramid may degenerate after unilateral cortical injury. Hamilton, loc. cit., believes that fibres may enter the opposite pyramid by way of the corpus callosum, and Schäfer‡ appears to have held a similar view. In reviewing the numerous observations which have been made upon the descending degeneration following

^{*} Hamilton, 'Roy. Soc. Proc.,' 1884.

[†] LANGLEY, "Recent Observations on Degeneration of Nerve Tracts in the Spinal Cord," 'Brain,' 33.

[‡] Schäfer, 'Quain's Anatomy,' vol. 3, 1893.

experimental extirpation of the motor cortex, it will be found that the majority of observers describe a slight amount of degeneration in the crossed pyramidal tract of the same side, yet no degeneration higher up of the corresponding pyramid (pyramid of opposite side). These results are based upon the cat, dog, and monkey; further on it will be seen that in man there is strong evidence of bilateral degeneration in the cord, following unilateral cortical injury.

François Frank, and Pitres* described in the dog bilateral degeneration of the crossed pyramidal tracts after lesion of the motor area.

Moeli† similarly observed slight degeneration on the same side in the dog.

BINSWANGER and MOELI‡ found in MUNK's dogs, in which the arm area had alone been removed, degeneration of the crossed tract only.

ZIEHEN§ examined three dogs, two and a half to three months after the extirpation of the fore-foot area and "nacken" area, and found degeneration likewise limited to the crossed tract. He therefore agrees with the last-mentioned observers, in opposition to those who maintain that there is bilateral degeneration of the crossed tracts after unilateral injuries. We may mention that the explanation of these divergent views is now finding its solution in a work by Dr. Mellus which will shortly appear from the laboratory.

Sherrington, who has largely worked upon the descending degenerations, maintains that not only in unilateral lesions of the cortex, but also in hemisections of the cord, there is some degeneration of the crossed tract upon the same side, his explanation of this, by supposing there is a re-crossing of pyramidal fibres, is that now usually accepted. As regards hemisection of the cord of the cat, I have not observed any degenerate fibres in the opposite crossed pyramidal tract.

MOTT¶ states that in a hemisection of the spinal cord of two monkeys, he was not able to satisfy himself of the existence of re-crossed fibres.

Homen,** on the other hand, describes a condition similar to that of Sherrington after hemisection.

TOOTH, †† in a hemisection of the chord of the monkey, found below the lesion only a few degenerate fibres in the cerebellar tract of the opposite side.

- * François Frank, and Pitres (see 'Prog. Méd.,' 1880).
- † Moeli, 'Archiv f. Psychiatrie,' 14, 1883, and 'Neurolog. Centralblatt,' 1883.
- ‡ Binswanger and Moell, "Zur Frage der Secundären Degeneration," 'Neurolog. Centralblatt,' 1883.
- § ZIEHEN, "Secundare Degeneration nach Extirpation motorischer Rindenregionen," 'Archiv f. Psych.,' vol. 11, 1887.
- || SHERRINGTON, "On Secondary and Tertiary Degenerations in the Spinal Cords of the Dog," Journal of Physiology, vol. 6, "On Nerve Tracts Degenerating Secondarily to Lesions of the Cortex Cerebri." *Idem*, vol. 10.
 - ¶ Mott, "On Hemisection of the Spinal Cord in Monkeys," 'Phil. Trans.,' 1892.
- ** Homen, "Contribution expérimentale à la Pathologie, et à l'Anatomie pathologique de la moelle épinière," 1885.
 - †† TOOTH, "Secondary Degeneration of the Spinal Cord," 1889.

SCHÄFER* early showed that unilateral cortical injury in the monkey might be followed by slight degeneration in the crossed tract of the same side—especially when the marginal convolution was injured; and later his assistant, France,† confirmed the bilaterality.

LOEWENTHAL, in the case of Schiff's dogs, found bilateral degeneration.

One gathers also from the papers of MARCHI, and MARCHI and ALGERI, that there is slight degeneration in the crossed tract of the same side after unilateral cortical injury.

TOOTH (l.c.) found in the monkey very slight degeneration in the crossed tract of the same side.

SANDMEYER§ found slight degeneration of the crossed tract on the same side as the lesion in dogs with unilateral motor cortical injuries; he used the method of MARCHI.

MAX HERZ | demonstrated bilateral pyramidal degeneration after the removal of the motor area in the monkey.

Schiff, in a recent paper on removal of the motor area in young dogs, observed some atrophy upon the same side as the lesion.

MURATOFF** has, still more recently, using the Marchi method, described the usual bilateral degeneration in the cord following unilateral injury to the cortex of the dog. He describes at the decussation the passage of degenerate fibres into the crossed tract of the same side as the lesion. There is, therefore, a bifurcation of the pyramidal tract at the decussation. In the preceding pages I have described a similar bifurcation, taking place in the cat, and Dr. Mott has also observed the same. At the present moment Dr. Mellus is engaged in the Pathological Laboratory of University College in accurately mapping out the extent of the bifurcation in monkeys in which definite portions of the motor cortex have been removed. His results, coupled with those of the previous observers and with my own in the cat, will go very far towards proving with certainty that apparently all the fibres in the crossed pyramidal tract on the same side as the injury are due to the bifurcation of the degenerate pyramid at the decussation.

In the cat, the amount of degeneration in the crossed tract of the same side as the

- * Schäfer, 'Journal of Physiology,' vol. 4, 1883.
- † France, "On the Descending Degenerations which follow Lesions of the Gyrus Marginalis and Gyrus Fornicatus in Monkey," 'Phil. Trans.,' 1889.
- † LOEWENTHAL, "Des dégénérations secondaires de la moelle épinière consécutives aux lésions expérimentales médullaires et corticales," I.D., 1885, and ref. in 'Neurolog. Centralblatt,' 1886.
- § Sandmeyer, "Secundare Degeneration nach Extirpation motorischer Centra des Hundes," 'Neurolog. Centralblatt,' 1891.
 - MAX HERZ, 'Neurolog. Centralblatt,' 1892, p. 192.
- ¶ Schiff, "Ueber secundäre Degeneration des Pyramidenseitenstranges bei Hunden," 'Centralblatt f. Physiologie,' April, 1893.
- ** Muratoff, "Secundäre Degeneration nach Zerstörung der motorischen Sphäre des Gehirns in Verbindung mit der Frage von der Localisation der Hirnfunctionen," 'Archiv f. Anat. u. Phys.,' 1893, Heft 3 und 4.

lesion is exceedingly slight, notwithstanding that the whole hemisphere has been removed. This coincides with the small bundle of fibres which does not cross at the decussation but curves round into the lateral column of its side. On account of their sparseness it is difficult to demonstrate these fibres at the bifurcation, unless a complete series of sections is made through the decussation; and although I have only recognized them in three or four examples, yet I feel sure that a more thorough examination of the decussation would reveal their presence in all cases. Their comparative fewness in the cat is well worthy of note.

I at first thought that the solution of the recrossed fibres of Sherrington would be found in the direct lateral columnar fibres described in the preceding pages. This I have now shown is not completely the case, seeing that they do not come from the cortex, and that they can be readily distinguished by their size from the pyramidal fibres, figs. 4 and 5, Plate 3. Their explanation in cases of cortical lesions is probably the one now brought forward.

Our knowledge of bilateral degeneration in man after unilateral cortical injury is not thorough. Following upon Flechsig's papers upon the precise mapping out of the pyramidal paths, Pitres* brought forward several cases of bilateral lateral sclerosis after unilateral cortical injury, and, since these, this variation has been often encountered. But there is no information to say upon what the absence or presence of the degenerate fibres on the same side as the injury depends, or whether the latter bear any relation to the presence or absence of a direct pyramidal tract. Mannkopf† has carefully described a case in which sudden hemiplegia was followed by complete recovery of the legs and partial of the arm. Death shortly afterwards occurred, the left arm being cedematous. Part of the right motor area was affected. There was degeneration of the left crossed pyramidal tract, but none in the right anterior or lateral tracts. Other similar cases have been recorded.

The Direct Pyramidal Tracts.—We have seen that there is no direct anterior pyramidal tract in the cat, although in those cases in which the fibres in the posterior longitudinal bundle and in the antero-lateral columnar tract are degenerate, an appearance of direct pyramidal fibres is simulated. There is no direct pyramidal tract in the dog (Sherrington and numerous other observers). There appears to be no direct anterior pyramidal tract in the monkey. I have assured myself from normal sections that there is no direct pyramidal tract in this animal comparable to the tract usually described in man. Similarly a direct pyramidal tract has not been found after motor cortical extirpation. Needless to say, a unilateral lesion in the medulla or cord, which passes through the upward continuation of the anterior column or through this column in the cord, will give rise to a descending degeneration

^{*} Pitres, "Les scléroses bilatérales de la moelle épinière consécutives à des lésions unilatérales du cerveau," 'Archives de Physiologie,' 1884.

[†] Mannkopf, "Beitrag zur Lehre von der Localisation der Gehirnkrankheiten, von der secundären Degeneration, &c.," 'Zeitschrft. f. klin. Med.,' 1884.

in the anterior column occupying the position of a direct pyramidal tract, but this degeneration has no relationship to the pyramidal system. Nevertheless, even in these animals the two systems have been confounded, and neurologists have spoken of a direct pyramidal tract in the dog. In man the confusion is much greater, observers stating that the direct pyramidal tract may be followed to the lumbar region, because they have seen, after injury of the spinal cord, a degenerate anterior column. In man, since the time of Ludwig Türck, and in spite of the beautiful monograph of FLECHSIG, a great deal of uncertainty exists concerning these tracts. Thus let it be pointed out that, whilst Flechsic states that an anterior and lateral tract may be demonstrated anatomically in 75 per cent. of all cases, he at the same time brings forward nine cases of descending degeneration in order to compare them with the anatomical results, but in three out of the nine cases the degeneration was confined to the crossed pyramidal tract. It has been assumed that the direct pyramidal tract varies in man, sometimes extending to the cervical region, at other times to the dorsal, or even lumbar, regions. If such an assumption is true, and it is certainly correct if FLECHSIG'S interpretation of his embryological results is the correct one, then it tends to divest the direct pyramidal of any definite function, such, for instance, as that surmised by Hughlings Jackson. On the other hand, some observers believe that the direct pyramidal tract is due to tardy decussation. In the cat and dog, as just stated, there certainly is no direct pyramidal tract, and in the monkey, although a few fibres may perhaps continue down in the anterior column after the decussation, there certainly is no direct pyramidal tract comparable to that seen in degenerations in man. And if one reviews some of the very numerous cases of descending degenera tions, either secondary or primary, in man, one is greatly struck by the irregularities of the anterior pyramidal tract; in some cases it is present, in others absent; in some cases the degenerate tract is small, in others large, and passing insensibly into the antero-lateral column.

FLECHSIG, WESTPHAL, KAHLER and PICK, STRÜMPELL, OPPENHEIM and others, in their descriptions of the simple and combined "system" scleroses of the cord, signal numerous irregularities, indeed, the first-named observer appears to divide the sclerose into systematic, asystematic, and mixed. In these cases the pyramids above the decussation may be normal, whilst below, a lateral crossed tract or a lateral and anterior pyramidal tract, or both crossed tracts, or both lateral and one anterior tract may be degenerate.

When the above facts are taken into consideration, it will be understood that the direct pyramidal tract in man still wants considerable explanation. It might be thought that the degenerate fibres in the anterior columns, close up to the pyramids (fig. 3, Plate 3), and derived from the posterior longitudinal bundle and raphé, might furnish some explanation, but this cannot be the solution, as we have seen that the fibres in question do not come from the cerebral hemispheres. Muratoff has made the suggestion at a recent meeting of the Moscow Neurological Society, that the

direct pyramidal tract in man is represented in the lower animals by the fibres of the pyramid which curve round to the pyramidal tract of the same side.

Topography and Connections of the Pyramidal Tract.—In the hemisphere cats, the whole of the crusta is degenerate and atrophied, and in the cats with the motor area removed, the degeneration is nearly as complete, a small portion of the innermost part of the crusta remaining free. At the level of exit of the IIIrd nerves, and at a slightly higher level, a few degenerate fibres may be seen passing directly backwards from the external portion of the crusta to the region of the corpora quadrigemina; similar fibres have been observed by Muratoff (loc. cit.). I also agree with MURATOFF that a few fibres may be seen leaving the degenerate pyramid in the medulla at its inner and posterior angle, but there is no definite bundle, and I have not been able to trace any of these fibres to nerve roots, nor, indeed, at any level of the pyramidal tract have I seen such a connection, a connection, for instance, between the pyramid and the descending root of the Vth or the nuclei of the Vth and VIIth nerves. In the pons I have not been able to show degenerate fibres leaving the pyramid to turn into the cerebellum. With these fibres which leave the pyramid must be coupled those from the crusta and internal capsule already As seen from the photographs, the crossed pyramidal tract has a somewhat round outline and is fairly compact. Compared with the monkey it is much less extensive. In configuration in the cervical region the pyramidal tract of the monkey differs markedly from the cat. Thus in a section of the cervical cord of the monkey after removal of the motor cortex (Schäfer and France's case), a distinct patch of degeneration may be seen on the outer side of the lateral cerebellar tract, the latter thus dividing the pyramidal tract. Sherrington has drawn attention to this ('Journal of Physiology,' 1889 and 1893), as also France. Coinciding with this, Mott ('Phil. Trans.,' 1892) describes the direct cerebellar tract leaving the periphery in the upper cervical region.

It is an old observation that the so-called pyramidal area is greater after a hemisection in the cord than after lesions of the cortex. This is due to the fact that descending fibres other than those of the crossed pyramidal tract are cut across. At the same time, it appears to me that the degeneration in the pyramidal tract proper is more intense after hemisection than after removal of a hemisphere.

The Degeneration in the Cranial Nerve Roots.

Optic Nerve.—The optic tract of the right side is divided in removal of one cerebral hemisphere. Corresponding with this there appears to be complete blindness of the right eye, and slight curtailment of the field of vision of the left eye. I have reserved however for subsequent investigation the disputed point, whether in the cat there is complete decussation or slight bifurcation. In Goltz's dog, described by Langley and

GRÜNBAUM,* the lesion in the region of the root of the optic tract is much less than in my cases. This will account for the fact that, whereas Goltz's dog could see with the right eye, my cats could not.

IIIrd Nerve.—The third nerve appears frequently to be injured after its exit from the mesencephalon. The root and the oculo-motor nucleus usually escape injury. I have not been able to demonstrate fibres from the region of the posterior corpora quadrigemina or from the posterior commissure entering either of the IIIrd nerves. Nor have I traced a certain connection between the posterior longitudinal bundle and these nerves.

Vth Nerve.—The descending root of the Vth nerve appears to commence in a focus at about the level of the upper oculo-motor nucleus and immediately behind it; it does not stand out, however, as a well-marked bundle of degenerating fibres till just below the level of the IIIrd nerves. As will be seen in fig. 1, the starting point of MEYNERT'S decussating fibres and of the descending root of the Vth appear almost to coincide. The ascending root is of very large size, increasing as it ascends and at the level of exit of the nerve sweeps out together with the fibres of the descending root which join it anteriorly. We have already described that in one case, owing to the extension of the lesion, the ascending root was injured, and that a considerable descending degeneration could be traced in it to the cord. This is therefore in accord with His, who calls it a descending root. Further, Herzen and Lewenthal[†] did not observe ascending degeneration of the ascending root of the Vth after its division at the junction of the medulla and cord in the cat. Tooth also describes descending degeneration. Sherrington, in a case where the cord was partially cut at the level of the 1st cervical, found degeneration of the Vth bundle below the lesion and none above.

The Degenerations in the Brain following Removal of a Cerebral Hemisphere or the $Motor\ Area.$

In the "Journal of Physiology" for 1890, Langley and Grünbaum published an account of the degenerations following removal of a cerebral hemisphere in the dog; the dog having been operated on by Goltz, and exhibited at the Physiological Congress in Basle in 1889. These observers likewise describe complete degeneration

- * Langley and Grünbaum, 'Journal of Physiology,' 1890.
- † HERZEN et LEWENTHAL, 'Archives de Physiologie,' vol. 7.
- ‡ Тоотн, 'Journal of Physiology,' 1892.
- § Sherrington, 'Journal of Physiology,' 1893.

|| In hemisection of the mesencephalon, I have observed very marked atrophy of the cerebral hemisphere on the same side, the internal capsule being greatly reduced in size. Spitzka has observed the same, following a similar lesion in the new-born cat, and, in addition, observes that the right half of the cerebellum was smaller than the left. I am reserving for subsequent work the changes in these cases.

of the pyramid, considerable atrophy of the substantia nigra, of the tegmentum, and of the grey matter of the aqueduct on the side of the lesion. The left anterior corpus quadrigeminum, the internal and portion of the external geniculate body were present on the left side. In my cases, these are usually all involved by the lesion (see optic nerve). They describe considerable degeneration of the posterior commissure and some degeneration in Meynert's bundle (not Meynert's decussation) on both sides. In my cases, the posterior longitudinal bundle appeared normal on the two sides. They describe the corpus callosum and anterior commissure as being much smaller than normal. It may also be mentioned here that LANGLEY and GRÜNBAUM state that the signs of degeneration, though distinct, were not very great in the crossed pyramidal tract of the opposite side of the cord. Recently MURATOFF* has described by the Marchi method the degenerations of the corpus callosum following removal of the motor cortex, or after section of the corpus callosum. He describes beneath the transverse fibres of the corpus callosum, longitudinal fibres on each side, to which he has given the name of fasciculus subcallosus, and which he regards as longitudinal association fibres between the lobes of the cortex on the same side. He describes partial degeneration of it after removal of the motor cortex. In those cats in which I have removed the motor area, as before stated, I have seen its atrophy on the side of the lesion, but only a few medullated degenerate fibres in it.

In the corpus callosum, he describes the commissure fibres passing from the seat of lesion to corresponding convolutions on the sound side, passing through the internal capsule, but not turning down in it; he adds that the appearances nearly completely disprove the Foville-Hamilton theory of the corpus callosum being the crossing between the internal capsule. As described in the preceding pages, we have noted a tendency to grouping of the transversely degenerate fibres in the corpus callosum. We have noted the fibres crossing the internal capsule, but we have not observed them turning down to get into the pyramidal tract. The pyramidal tract on the opposite side is always free from degeneration.

The degeneration of a bundle of fibres in the dorsal upper third of the pineal body, accords completely with the anatomy of this body, as described by Darkschewitsch.

- * MURATOFF, 'Neurolog. Centralblatt,' 1892.
- "Secundäre Degenerat. nach Enfernung der motorischen Sphäre." 'Archiv für Anatomie und Physiologie, 1893. Heft 3 und 4.
- "Secundäre Degenerat. nach Durchschneidung des Balkens." 'Neurolog. Centralblatt,' November, 1893.
- † In the case of his corpus callosum dog, Muratoff describes the animal as sleepy and apathetic, and not readily roused; considerable incoordination. Unsteady, shaky gait. Dog appearing like one in which both motor areas had been removed. Some affection of sight, the animal running into obstructions. In one cat, in which Dr. S. P. Kramer and myself divided the corpus callosum, there were after the first few days, remarkably little symptoms, and apart from some photophobia, it behaved much as other cats. On one occasion, when disturbed by the presence of another cat, it was seized with severe epileptoid convulsions.
 - ‡ Darkschewitsch, "Zur Anatomie der Glandula Pinealis." 'Neurolog. Centralb.,' 1886.

As the degeneration shows, it contains functioning nerve fibres closely related to those in the posterior commissure, and it now remains to be seen whether it is the vestigial body it is usually described.

Note on the Corpus Callosum.—In addition to the preceding remarks upon the corpus callosum, it is stated by Professors Horsley and Gotch (Croonian Lecture) that Brown-Séquard found the middle half of the corpus callosum was excitable. The same investigator* states that excitation of the corpus callosum after removal of one hemisphere, causes movements on both sides, but especially upon the side of the remaining hemisphere. Mott and Schäfer† obtained the best excitatory results from the thin middle part of the corpus callosum; they state that there is no definite grouping of the fibres, and that the fibres do not pass directly into the internal capsule, but enter the grey cortex upon the opposite side. According to Sherrington‡ the fibres coming from a cortical lesion, tend to scatter after crossing over in the corpus callosum, and do not chiefly pass between identical areas of the two hemispheres. Our own researches show a slight grouping of the fibres, and a more or less scattered distribution to the opposite cortical convolutions; we have no evidence for stating that fibres cross between identical convolutions, nor have we observed any fibres going to the basal convolutions.

PART II.—SYMPTOMS OF THE ANIMAL DURING LIFE, AFTER (1) REMOVAL OF THE CEREBRAL HEMISPHERE; (2) REMOVAL OF BOTH CEREBRAL HEMISPHERES;

- (3) Removal of the Motor Area; (4) Division of the Crus Cerebri;
- (5) Removal of a Lobe of the Cerebellum; (6) Hemisection of the Spinal Cord.

Symptoms following Removal of a Cerebral Hemisphere.

Observations have been made upon thirty-five cats, and the average symptoms are found to be constant. These thirty-five cats represent the successes out of very many failures which I do not include, namely, animals which have died after the operation or within the three subsequent days. The average mortality after the operation has been high. Sometimes recovery followed after a continuous series of operations, at other times the reverse happened. Much depends upon the animal,

^{*} Brown-Séquard. "Faits montrant que la galvanisation de la surface de chaque hémisphère cérébral agit sur les muscles des membres du côté opposé par deux voies distinctes." 'Comptes Rendus, Soc. de Biologie,' 1879.

[†] Mott and Schäfer, "On movements resulting from faradic excitation of the cortex." 'Brain,' 1890.

[‡] Sherrington. "Some tracts degenerating secondarily to lesions of the cortex cerebri." 'Journal of Phys.,' 1889.

the older animals at first stand the shock better than the younger ones, but the younger ones, when they survive the operation, heal much sooner.

Cause of Death.—In the first two experiments the respiration ceased, artificial respiration, however, brought the animals round, and they recovered completely. In subsequent operations the stoppage of respiration never occurred. Some animals never rallied from the operation, dying comatose. In others, death was due to considerable extravasation in the remaining hemisphere or in the theca. But, it must be also mentioned, that considerable hæmorrhage might occur around the dangerous region of the pons without entailing death; this I have verified on several occasions in post-mortems made a long time after the operation. In six cases in succession, death occurred on the second or third day from carbolic acid poisoning, the symptoms being distinctly irritative. A very considerable number of deaths occurred within the first week through failure of healing per primam.

Under the most favourable circumstances the animal may be able to walk around its cage two hours after operation, but weakness upon the opposite side (right side always) is readily perceptible, there being usually some wrist drop and occasional stumbling. In other cases, the animal is able to progress on its four legs twelve or twenty-four hours after operation. Occasionally rotation fits or choreiform movements occur in the first two or three days.

If the animal remains in a torpid condition it usually indicates *pressure*, due to serous fluid or pus; the animal should therefore be closely watched so that pressure may be relieved, or the cavity washed out as early as possible. Recovery very often occurs in these cases, but the weakness upon the opposite side persists much longer. After complete recovery the animal may begin rapidly to waste in the first or second month, and usually dies in consequence.

Average Symptoms after Recovery.—The most striking phenomenon is the absence of marked symptoms. The animals may be very active, running and climbing as in the case of the normal cat; they mew and purr. When their gait is carefully studied, the slight abnormality becomes apparent; they tend to turn always towards the left, they jump awkwardly, and ascend stairs with the left foot first. When pushed to one or other side, weakness upon the right side may be detected; this may also reveal itself in occasional wrist drop. The weakness appears more marked in the case of the fore paw than in the hind limb. Complex acts are performed by the right fore-paws; the animal often spontaneously washes its face with that limb; and reflex movements can be readily elicited on either side by scratching behind the ear. I have not observed much increase of this reflex (Brown-Séquard) phenomenon on the operated side. When the animal is held up, in the position, for instance, that is adopted for testing the knee-jerks, the right limb usually lies extended, the left being flexed upon the abdomen after the usual manner of cats.

The motor defects are by no means so obvious as those of sight. The sense of perception in the normal cat is not good, comparing very unfavourably with the dog,

whilst with one hemisphere the diminution of this sense is the most striking feature. As far as I have been able to test, there is complete blindness in the right eye, and considerable diminution in the left eye. This loss of sight on the right side, coupled also with the probable loss of hearing on that side, accounts for the slightly twisted position of the head, especially marked when the attention of the animal is engaged; the animal turns the left half of the face upwards; when following objects, such as meat or milk, or the attendant, it turns to the left, and when called it turns in the same direction. There is no mistaking that it does not use the right eye, and that it is at the same time awkward with the left one. Tested carefully with a small red disc, this may be passed across the field of the right eye, and slightly over the middle line into the field of the left eye, before notice is taken of it; approached, on the other hand, from the left side, perception takes place at a wide angle.

Tested with a powerful beam of light, a slight pupil reflex and not maintained for long, could be obtained in the right eye, and readily in the left eye. With ordinary light and shade the movements of the left pupil were accompanied by those of the right eye. Thus when a beam of light was projected into the left eye, contraction took place in both, and similarly dilation on shading the left eye; in addition, when the left eye was shaded, the right pupil dilated in spite of a beam of light.

The knee-jerks were tested in every instance, yet the results are unimportant; perhaps there was slightly more clonus upon the right side, but the *force* of the movements was distinctly less; it was therefore difficult with this combination to gauge anything definite. A much more striking symptom appeared to me to be the above-mentioned extension of the right limb, or rather absence of flexion.

Sensory Changes.—The blunting of sensation on the right side was striking. Thus over and over again the animal might be observed to accidentally place its right fore or hind limb into its drinking water and not remove it, whilst if the same occurred with the left limbs they were immediately retracted. Similarly, with the needle or with the clip, and in many other ways, the obvious dulling of sensation, and the tardiness of reflex action, could be demonstrated on the right side. On the left side I often thought the sensibility was increased. Absinthe, as might have been expected, served in many instances to bring out these contrasts, and in the graphic record of the movements elicited by that agent, we have, I think, a measure of these differences.

The act of feeding was performed with the greatest difficulty, and to save time the cats were invariably fed with milk, in a syringe, which was thrust into their mouth, as in the case of pieces of meat. If the animal was left to itself with its food it was only by accident that it discovered its milk or meat. Eating was very awkward; there appeared little if any sense of smell and taste on the right side; prehension and chewing were very defective. Compared with cats with hemisection of the cord, the paralysis and loss of sensation is much less profound. Compared with cats in which one lobe of the cerebellum is removed, the incoordination is less, and the

amount of paresis greater, for the same date; thus there is no wrist drop in the cerebellum cats.

Comparison of the Anatomical Changes with the Symptoms during Life.—The average degenerative changes, which we have already discussed, may be summed up as:—

- 1. Complete degeneration of the left *pyramid*, very slight *bifurcation* at the decussation, the main mass passing over to form the right crossed pyramidal tract.
- 2. Presence of degenerate *lateral columnar fibres* on the right side, in some cases, and usually in a less degree upon the left side.
- 3. Degenerate fibres in posterior longitudinal bundle on left side, and of anterolateral columnar fibres on the right side.
 - 4. Degeneration of the descending root of the Vth and VIIth nerves on the left side.
- In Cat No. 1, recovery took place rapidly, but about the thirty-fourth day the animal became very weak; there was almost complete paralysis of the hind limbs, and marked weakness of the fore feet. The anatomical changes included the presence of two well-marked direct lateral columnar tracts, together with the other average pathological changes.

Cat No. 2.—Animal remained comatose after the operation, and nine days afterwards suppuration was indicated by the distension of the wound. The tension was relieved, and the cavity washed out. The animal had never regained the proper use of its feet, and was killed on the nineteenth day, the symptoms having grown worse.

At the post-mortem, pus was found in the left cranial cavity, with extension into the ventricles of the right side.

Microscopic examination showed great extension of the wound in the mesencephalon, producing a very complete unilateral lesion extending to the upper part of the pons, with here and there scattered minute foci of suppuration. Corresponding to this both direct lateral columnar tracts showed very marked degeneration, and the mesial antero-lateral columnar fibres were extensively altered; the other usual degenerations were present.

Cat No. 5.—This animal remained in a stupid condition, and had not regained the use of its limbs on the fifth day. It was then seen that the wound was tense, and in consequence an incision was made, and a very large quantity of pus evacuated. After washing, suppuration ceased, and the animal picked up, and at the end of one month could walk fairly well, but still showed more weakness upon the right side than cats which recovered without abnormalities of healing. In this case microscopical examination showed considerable extension of the wound, and two well-marked direct lateral columnar tracts, in addition to the usual changes.

Cat No. 12.—This animal made a good recovery, but at the end of a fortnight developed choreiform movements upon both sides, most marked, however, in the fore limbs. The movements were increased by pressure on the scar. Post-mortem the wound was found healthy, but there were numerous extravasations along the cord.

Microscopic examination showed that the degenerative changes were mostly limited to the pyramid, there being very few fibres in the mesial and lateral columns.

Cat No. 21.—The animal recovered after the operation, but became ill and paralysed, and died on the fourteenth day; the wound was found to have suppurated.

Microscopic examination showed most extensive changes in the mesencephalon; in this region there was almost complete transverse myelitis; the pyramid on the side of the lesion was completely degenerate, whilst that upon the opposite side was partially so; both posterior longitudinal bundles, both antero-lateral columnar bundles, and both lateral columnar bundles contained very few normal fibres. The cord thus presented the typical results of a transverse myelitis in the mesencephalon.

Other Examples.—In those cats which made a rapid recovery, and which presented the average symptoms described in the preceding pages, the anatomical changes were limited to one pyramid, to certain fibres in the posterior longitudinal bundle, anterior and antero-lateral columnar tracts, and descending root of the Vth.

It will be gathered from these illustrations that the extent of the degeneration following removal of a cerebral hemisphere depended upon the severity of the injury in the mesencephalon. Thus, in those cases where the lesion did not exceed a complete hemisection at the level of the IIIrd nerves, there followed the average degeneration changes, viz. —Fibres in posterior longitudinal bundle on same side. Descending root of Vth on same side. Pyramid on same side. Anterior and anterolateral columnar fibres on opposite side. On the other hand, the more extensive the lesion transversely, the more bi-lateral was the degeneration. I never found any disproportion between the size of the lesion and the resulting change, a fact which proved the accuracy of the Marchi method.

The severity of the symptoms, it will also be observed, is related both to the condition of the wound and the resulting degenerative changes. In those cases where the recovery of the paralysis on the right side was not good, there was extensive degeneration of the anterior and antero-lateral columnar fibres. But, as the degeneration in these columns is only a measure of the severity of the wound, the most useful comparison is that between the condition of the wound and the symptoms. At repeated autopsies it was found that a limited suppuration not producing pressure was quite compatible with rapid recovery of the paresis of the right side. When the cavity became distended, however, the paretic symptoms rapidly increased, as in Cat 5.

Thus, in the absence of pressure, a degenerate pyramidal tract and degenerate fibres in the anterior and antero-lateral columns are compatible with a motion and use of the right limbs little inferior to that in the normal animal.

The severe effects following a comparatively rapidly-produced pressure are well known. Malinowsky* produced abscesses in the motor area of the brain followed

^{*} Malinowsky, "Ueber küustlich erzeugte Gehirnabscesse," 'Centrlb. f. d. Med. Wiss., 1891,' No. 10.

by paralysis; he found, however, that if the abscess, together with the surrounding motor cortex were removed, recovery took place. Schrader's* experiments upon artificial tuberculosis of the brain also gave the same results. The slowly-growing tumour, on the other hand, produces little effect, and in striking illustration of this may be mentioned the observations of Roth,† who records numerous cases in animals where the cranial cavity was for the most part occupied by bone tumours, without giving rise to paresis.

In man, Mahaim; describes a case in a child in whom one hemisphere was the seat of an atrophic change of long standing, the major portions of the external capsule and of the cerebral peduncle and motor convolutions being involved, yet in spite of the fact that one pyramid was absent, the child showed no signs of paralysis; it walked normally, there were no spastic phenomena, but the left arm was a little contracted; there was no loss of sensibility. Mahaim regards this case as proving that each pyramid is in union with both halves of the cord. The experiments of Goltzs were the first, however, to show clearly that in the dog one hemisphere might be removed without any serious paresis.

Goltz's Experiments.—The results of my experiments confirm the classic observations of Goltz upon the dog, and as this enquirer has already dealt with the views of others which bear upon the subject, it will be useless for me to repeat them here. Goltz's conclusions are briefly as follows:—

There is no approach to a lasting paralysis upon the opposite half of the body. The animal does not use the opposite limbs with the same readiness as the others. There is not complete loss of sensation upon the opposite side, but there is dulling of sensation; there is muscular consciousness, and there is a tendency to turn to the left. There is impairment of vision in the opposite eye (hemiamblyopia of LOEB). In my experiments on the cat, the loss of vision in the right eye appeared complete, and this may be due, as mentioned elsewhere, to more complete destruction of the roots of the optic tract on the left side. According to Goltz, each cerebral hemisphere is in connection with the voluntary muscles of both halves of the body. It appears, however, that the connection between one cerebral hemisphere and the muscles of the opposite half of the body is more convenient than that on the same side. Hence a dog, whose left hemisphere is destroyed, prefers to use the left paw, because the will impulses from the right hemisphere flow by more convenient paths to the left limbs (Langley and Grünbaum, loc. cit.). Later on, we shall have more to

^{*} Schrader, "Ueber die Stellung des Grosshirns im Reflexmechanismus des Central-Nervensystems der Wirbelthiere," 'Archiv f. Path. u. Pharmak.,' B. 29, and elsewhere.

[†] Roth, "Ueber eine intracranielle Dental-Exostose von einer Ziege," Diss., Zurich, 1888.

[‡] Mahaim, "Ein Fall von secundärer Erkrankung des Thalamus opticus und der Regio subthalamica," 'Arch. f. Psych.,' vol. 25.

[§] Goltz, "Ueber die Verrichtungen des Grosshirns," Pflüger, 'Archiv f. Physiologie,' vol. 42.

^{||} Goltz, "Removal of whole Brain," Pflüger, 'Archiv f. Physiologie,' vol. 51, 1892.

TANGLEY and GBÜNBAUM, 'Journal of Physiology,' vol. 11.

say concerning the conduction of these impulses and their paths; but as far as we have gone we have seen reason to believe that one pyramid is distributed to both halves of the cord, owing to bifurcation at the decussation, and that, in the cat, numerous uninterrupted direct commissural fibres descend from the important centres in the quadrigeminal region to the lateral and anterior columns of the cord.

Symptoms following Removal of both Hemispheres.

I have not yet succeeded in keeping the animal alive any length of time after the operation, the animal dying on the second or commencement of the third day. In my cases the hemispheres have been removed at one operation, whilst Goltz in his example removed the brain in portions at different dates. The cats had not time to regain the proper use of their limbs, though violent incoordinate movements were common. A noticeable feature was the power of the animal to utter cries. hemispheres in Goltz's case were not so radically removed as in the above cases, but they nevertheless demonstrated the complex nature of the acts which could be performed in the absence of nearly all the fore-brain. The brainless dog could walk, showing no inclination to turn to the right or left as in the case when one hemisphere alone was removed; it could show an appreciation for stroking, and for heat and cold, and performed numerous reflex acts. There was the same difficulty in eating in the commencement that I have always observed in my cats with one hemisphere, and which I have attributed to the extension of my lesion in the quadrigeminal region. GOLTZ'S dog without hemispheres furnishes a striking example of the importance and independence of the paths of communication between the higher centres in the mesencephalon and medulla, and in the cord in the Carnivora. In the lower animals, as Schrader and others have shown, the independence is, as is well known, much greater.

Symptoms following Removal of Motor Area upon one side.

In these animals, as described earlier, the anatomical changes were entirely confined to one pyramid; there was no degeneration of the direct paths descending from the quadrigeminal region. The symptoms were proportionately slight, the animals after a temporary paresis, as shown by slight wrist drop, appearing quite normal. There was no affection of sight, and no abnormality of walking or holding the head, or of feeding. Thus there is a considerable contrast between a cat with its motor area removed and a cat without a hemisphere, or its equivalent (in many respects) a hemisection in the quadrigeminal region.

Goltz describes, that in dogs in which he had removed the anterior (motor) portions of both hemispheres, there was no paralysis, the movements were clumsy and exaggerated. The difficulty of feeding was marked. He makes the important observation that, comparing a dog in which one motor area is removed with one in which both are

absent, the symptoms of the latter do not represent the sum of those of the former animal. On the contrary the symptoms are greatly aggravated, the animal cannot feed, "is very clumsy in its movements, and cannot make use of its 'Pfoten als Hände." He concludes that "aus diesen Erfahrungen muss man, glaube ich, schliessen, dass in der vordern Hälfte des Grosshirns symmetrisch gelegene Einrichtungen stecken, welche für einander eintreten können. Wird der eine Vorderlappen des Grosshirns zerstört, so bleiben die Bewegungen des Thieres nur so lange annähernd normal, als der symmetrische andere Vorderlappen unversehrt ist."

Symptoms following Division of the Crus Cerebri.

The operation is readily performed. A trephine hole is made over the occipital lobe, close to the tentorium, the dura mater is cut through, and a scalpel introduced between the tentorium and occipital lobe, and a cut made from the middle line forwards and outwards. The incision usually passes between the anterior and the posterior corpus quadrigeminum, the tegmentum, and if deep enough the crusta; the incision is thus a hemisection of the mesencephalon.

I have performed the operation in two cases; in both experiments the incision was very complete. In one case (the first) the symptoms were more marked than in the other.

In the first case the cat had a rotation fit (on its long axis) away from the side of the lesion, when disturbed or on attempting to move. This phenomenon lasted one week, during which time the hemiplegia disappeared. As in the hemisphere cats, the animal moved to the left, and appeared quite blind and deaf upon the right side; feeding was extremely awkward. There remained perceptible weakness upon the right side as well as distinct loss of sensation. The cat held its head in the twisted position observed in some of the hemisphere cats, only in a more exaggerated degree. Scratching the left side of the face elicited a most powerful scratching movement of the left leg, the cat on one occasion rolling over on its back, as in the Brown-SÉQUARD guinea pig. This phenomenon has I believe been observed in cats after hemisection of the cervical cord. In the second cat the hemiplegia was only present on the first day after the operation, but slight weakness and loss of sensation remained as in the other cat. The animal turned to the left, held its head in the characteristic position, appeared blind and deaf on the right side, and had to be artificially fed at first. There were slight rotation fits in the commencement. In both animals there was nothing to remark about the knee-jerks, but the right leg showed the extension phenomenon as in the hemisphere cats.

The second cat developed cedema of the right foot; this was the only marked lesion which I have met with in my operations which might be put under the heading of trophic influences. It is worthy of note that, owing to the cedema, portions of the

right limb were hyperæsthetic, whilst sensation as a whole upon the right side was lowered.

It will be seen that the symptoms described above are for the most part quite like those of the hemisphere cats. The rotation fits and the twisted position of the head were, however, much more strongly marked than in the latter animals. It would of course be difficult, with the slight knowledge before us, to attempt an explanation of the phenomenon. It occurs as is well known in lesions of the cerebellum (see later). In the above cats the superior cerebellar peduncle would have been divided after its decussation, and, therefore, ascending impulses from the cut surface would pass to the left hemisphere, the hemisphere the connections of which with the cord are cut off by the incision. Or the impulses might have descended from the cut surface by the direct fibres on the left side, coming from the quadrigeminal region; if this were so, one would have expected to see this phenomenon in the hemisphere cats. Impulses might have passed from the left hemisphere across the corpus callosum to the opposite hemisphere; in favour of this might be advanced the fact that extensive degeneration changes had immediately followed, especially in the first cat, in the left hemisphere after the incision, and that the irritation set up by the changes might have been transmitted across the corpus callosum.

Symptoms following Hemisection of the Cervical Spinal Cord.

The hemisection was made in the cervical region, on the right side, close under the decussation. The symptoms were similar to those which have been described by numerous observers. The paralysis on the right side was more marked and more persistent, especially in the leg, than in cats in which the left hemisphere was removed, or in which a hemisection was made in the quadrigeminal region. The difference between the paralysis of cortical and spastic origin has also been pointed out by observers. We have already seen, as others have seen, that the descending degeneration resulting from hemisection of the cord is greater than after cortical lesions; further, Homén* points out that complete hemisection gives rise to more persistent symptoms than section of the lateral column alone.

SUMMARY.—It will be seen, therefore, that there exists a relationship between the extents of the degenerations and the symptoms.

Removal of the motor area entails degeneration of the pyramid alone, and a temporary paresis; the animal appearing after a short time quite like the normal.

Removal of a cerebral hemisphere, or, what is nearly the same, a hemisection in the quadrigeminal region, gives rise to degeneration of one pyramid, and certain direct fibres which run into the anterior and lateral columns, and of certain fibres

^{*} Homén, 'Contrib. expérimentale à la pathologie et à l'anatomie pathologique de la moelle épinière.' Helsingfors, 1885.

which go to special cranial nerves. The symptoms are more pronounced, sensation is much altered, there is great difficulty of feeding.

Hemisection of the cervical spinal cord produces extensive degeneration of the anterior and lateral columns of the cord. There is at first hemiplegia, the vasomotor disturbance is much greater, and the sensory and motor paresis lasts longer.

Symptoms following Removal of a Lobe of the Cerebellum.

I have performed this operation in a large series of cats, but only succeeded in keeping a few alive beyond the second week. The operation is more serious than removal of a hemisphere, owing partly to hæmorrhage, and partly to the frequency of suppuration. I have only attempted to remove one lobe, viz., that on the right side.

The severity of the symptoms has varied greatly. In some animals the symptoms have been exceedingly slight, the cut showing little abnormality a few hours after the operation; in one case in which the lobe was completely removed no differences of motion or sensation could be detected on either side. It was more usual, however, to find some of the characteristic cerebellar symptoms. Rotation fits after the operation, or from irritation of the wound, were frequently seen; for the first few days there was unsteadiness of gait, which undoubtedly appeared more related to the right side (side of lesion) than the left; it could, in fact, usually be made out that there was distinct weakness of the right side. There is undoubted dulling of sensation on the right side, especially in the hind limb; this phenomenon had early attracted my attention, and still earlier that of Dr. Russell, working on other animals in the same laboratory. The weakening of sensation and motor power appears centred in the hind limb, and as previously stated I have not noticed wrist drop as in the case of hemisphere cats. The right hind limb is often placed obliquely under the body, and it is very easy to push the animal over on its right side; the animal ascends stairs with the left feet first, the right hind limb dragging, and, in running, instinctively seeks support on the right side by keeping close to the wall. In other cases I have noted unsteadiness and jerkiness of the right limbs. In one example the animal tended to fall to the left side; when running or performing any act, such as scratching, it appeared jerked over on to this side. We were not able to detect any differences in the knee-jerks.

To understand the differences of the kind of motor weakness in the hemisphere and in the cerebellar cats respectively, the two must be observed side by side. The weakness in the case of the one hemisphere cat is uncomplicated; on the contrary, that in the cat with one cerebellar lobe removed is intimately bound up with complex phenomena of incoordination. The weakness in the two cases is due to different causes, and it would seem that this is borne out by the anatomical changes. In the cortical case the pyramid is degenerate; in the other case it is intact; nor are there

any other marked descending tracts to the spinal cord, at least, in my cats. From the experimental side also, as will be seen, these differences are further brought out.

PART III.—RESULTS OF ABSINTHE STIMULATION.

Having, in Parts I. and II., had the opportunity of briefly comparing the facts of the functional and anatomical changes which result from a series of ablations of cerebral substance, it now remains to briefly record the results elicited by stimulation of the remaining nerve substance.

Mode of Research.—The stimulant employed has been in every case Absinthe, which, as is well known, from the researches of Marie, Magnan, Horsley, and Horsley and Gotch, acts as a powerful cerebral excitant. In the cat and dog injection of a few minims of this agent produces a series of fits, showing a striking resemblance to those seen in epilepsy. The fit commences in about 30 secs. after the injection of the absinthe, and is manifested by twitchings of the muscles of the eye, face, and ears, which are immediately followed by clonic and tonic spasms of the limb and trunk muscles; there is salivation, the urine is often passed, cries are frequent, and, finally, a state of unconsciousness may supervene. In the cat there is usually a most regular succession of fits at regular intervals of half a minute or longer; towards the end of the pause, slight stimulation heightens the intensity and rapidity of the onset of the fit. These toxic effects sufficiently closely resemble those seen in epilepsy to suggest a toxic origin in some cases of the latter, and to indicate the value of absinthe in the study of the seat of origin of the epileptic fit.

Methods of Procedure.—The absinthe excitation in each group of experiments was made both immediately after the operation (the animal being under an anæsthetic), and also in all cases, where possible, after complete recovery of the shock—that is, on the next day, or at some subsequent date. The following is a list of the experiments, of which a very great number were made:—

- 1. Removal of left hemisphere.
- 2. Removal of left motor area only.
- 3. Removal of both hemispheres or of both motor areas.
- 4. Removal of cerebellum or of right lobe.
- 5. Removal of right lobe of cerebellum, and opposite lobe of the cerebrum and vice versa.
 - 6. Hemisection of the mesencephalon.
- 7. Removal of one hemisphere, combined with section of left or right side of the cervical spinal cord.
 - 8. Section or hemisection of the spinal cord.

The animal having been anæsthetised, the extensor tendons of the fore-paws were exposed and freed; a stout ligature was passed round them, and connected to two equally calibrated simple steel spring myographs. By this means the slightest move-

ments of the extensor muscles of each fore-foot were recorded by the respective levers. In order to eliminate as much as possible the possible communication of movements of one side of the body to the other, great pains were taken to thoroughly fix each olecranon and each fore-paw, the cat-board being so adjusted to allow of this being readily done; in addition the shoulders were usually grasped in each hand, both in order to fix them and to feel the movements; at the same time the movements of both series of muscles were carefully followed with the eye. How little movement was actually communicated to the other side will be gathered from those tracings in which unilateral fits are recorded. Equality of calibration is very difficult, so that it is not easy in every case to ensure perfect symmetry of the fits on each side (as in normal cases, where the nervous system is intact), the levers on both sides rising and falling to the same degree. The levers recorded their movements upon a smoked surface, travelling at a slow rate of speed; the respiratory movements by a belt around the chest and Bert's tambour were also recorded, and, when necessary, the time. All the levers were as accurately adjusted in line as possible. The jugular vein was exposed, and two to four minims of absinthe injected, and the results recorded upon the travelling surface. Practice is necessary in order to judge of the right degree of anæsthesia necessary to give the best results. Too much absinthe has a narcotic effect, but doses of two minims may be repeated two or three times.

Description of Normal Tracing, Respiratory Curve.—A few seconds before the fit, the respiration is increased; this is a very characteristic premonitory sign. With the onset of the fit, a short series of deep inspirations are made, which is followed by a period of very shallow breathing; this, in its turn, is succeeded by one or two deep inspiratory efforts, and then well-marked, regular, and slow expiration and inspiration. The deep inspirations at the commencement correspond to the clonic stage of the fit, the shallow respiration to the tonic, and the commencement of the large slow respirations marks the cessation of the fit.

Muscle Curves.—When the two muscle curves are compared, it will be seen that the character of the fits is almost identical upon both sides. The movements of the left lever appear, however, more vigorous than those of the right—a circumstance which may depend upon various causes, amongst others, inequality of calibration; otherwise, both sides closely resemble one another. Each fit usually commences with a small series of powerful clonic spasms, gathering strength as they proceed; these give place to a very rapid succession of contractions, which build up an increasing but irregular tetanic contraction, which lasts for about twelve seconds, and which corresponds to the tonic phase of the fit; the lever then falls with considerable abruptness, although slight variations in regard to this do occur. Corresponding to the premonitory stage of quickened respiration, the muscle levers often record a few small twitches; this marks a period of heightened excitability.

1. Removal of Left Hemisphere.

Series A.—Absinthe excitation immediately after the Operation.

There is, as might be expected, general diminution of the intensity and duration of the fits, due to the loss of blood and shock generally. In a few cases the fits are unilateral, but in the majority they are *bilateral*. Evidence goes to show that this difference depends upon the state of the animal, the bilateral being associated with those cases in which the series of fits are prolonged, and in which there are other signs of marked vitality, whilst the unilateral occur in the enfeebled animal.

In studying the tracings of all operated animals, comparison should especially be made between the *initial fit*, the fits of maximum intensity, and the fits of slight intensity at the end of the whole series.

Fig. 6 represents the two first fits which followed the injection of the absinthe. There is a marked contrast between the first. Both start at the same time, but the

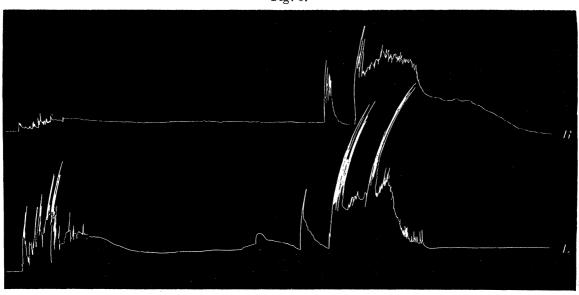


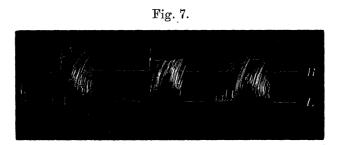
Fig. 6.

Left hemisphere removed and immediate absinthe excitation. Note the contrast between the initial fit on the right and left side.

fit upon the right side, corresponding to the lesion, is very small; that on the left side is fairly typical. In the second explosion, the fits more closely resemble one another; the contractions are, however, more powerful on the left side, clonus being conspicuous, whilst on the right side there is tonus.

Fig. 7 represents the fits of the middle period. On the right side there are a few premonitory twitches; on the left side they are numerous. Both sides start with a few initial clonic contractions, then tonus follows; but whilst on the left side the contractions which build up the tonus are powerful, and make wide excursions, which

show that impulses are descending strong enough to elicit further contractions from the already contracted muscles, on the right side the impulses are only sufficient to maintain a tonus; they are not strong enough to form stairs, although they may give rise to irregularities. As in both instances the levers rise and fall rapidly before and after the onset of the fit, so it may be assumed that the muscles are equally excitable in both cases, and that the differences in the tracings are due to the difference of the impulses passing down the cord.



Same tracing as fig. 6, but subsequent fits.

In a tracing of the fits approaching the end of the series, it will be seen that on both sides the number of contractions have been greatly reduced, that the rhythm is less regular, and the tonus has almost disappeared. Both sides compared, the strength of the contractions appears nearly equal, although, still nearer the end, those on the right side may get weaker; the *number* of contractions on the left side, however, is about double that on the right. If the tracing were followed further, it would be seen that many of the small fits are not represented upon the right side.

Towards the end of the experiment, the clonic fits give place to single contractions, occurring at regular intervals, and usually bilateral; they then insensibly, or after a long interval, pass into powerful asphyxial spasms, often more accentuated upon the right side than upon the left; they usually terminate with the "tail phenomenon."*

Summary.—There are bilateral fits. On the paretic side (right side) the initial fit may be much smaller than that on the left side, and in the subsequent fits tonus is more marked than clonus; the final clonic contractions are less numerous on the same side.

Series B.

In this series the left hemisphere was removed some days or weeks previous to absinthe excitation. The results are for the most part similar to those in the preceding group, the chief difference being, as might be expected, that the fits are more vigorous and simultaneous, and in many cases are equal on both sides. The animals experimented upon presented during life the symptoms described in Part II., and the tracings showed that the intensity of the fits was in proportion to the

^{*} See Schiff, Pflüger's 'Archiv,' and Horsley and Gotch, 'Phil Trans.'

action of the muscles of the weak side. The following are the chief features presented by the fits in the cats especially enumerated in Part II., p. 356, whose symptoms and anatomical changes have therefore been already studied.

Cat 1.—Two minims of absinthe were injected, and resulted in the production of a small fit, consisting of tonic spasms upon the left side, but only traces upon the right side. Spasmodic contractions subsequently occurred equally on both sides.

Cat 2.—Injected two and a half minims of absinthe. The respiration was rapidly increased, and was soon followed by a very small fit, felt well in the left limbs, and also slightly in the right limbs. After a slight attempt at another fit, death occurred. There was no spasm phenomenon. Cat was moribund at time of experiment.

Cat 12.—Three minims of absinthe were injected, and produced a fit, well marked upon the respiration and upon the left side; there were slight contractions of the muscles of the fore foot. Spasmodic contractions were very marked, and especially so in the right fore foot.

Cats 21 and 25.—Died before experimentation.

It will be gathered from the above experiments that the intensity of the fits is regulated by the condition of the animal; in each of the examples the cat was very feeble, being scarcely able to walk. One or two slight fits were obtained, and were almost entirely limited to the left side.

On the other hand, if the animal makes a complete recovery, and is well at the time of absinthe excitation, one rarely fails to obtain a series of well marked bilateral fits, as represented in the following tracings:—

Cat 6B.—Animal lived eighty-two days and had made a rapid recovery, and was perfectly healthy at time of experiment.

The tracing shows that the absinthe was followed by a rapid series of powerful explosions, which were soon followed by single contractions. On comparing the two sides it was seen that there was greater equality than in the series A. There was less difference in the initial fits; on the other hand the fits were more powerful on the left, and there was an extremely rapid clonus, coupled with tonus.

Summary.—In cats which have completely recovered from this operation, the fits are powerful on both sides, but differences can still be made out between the two sides.

2. Removal of Left Motor Area.

In two cases tracings were obtained from animals which had made a complete recovery after the removal of the anterior portion of the left hemisphere. The tracings resemble those of the B series above; there is on the whole, however, less difference between the two sides.

Summary.—The fits on the right and left sides closely resemble one another, there is considerable clonus upon the right side as well as upon the left.

3. Removal of Both Hemispheres.

Series A.—Division of Both Peduncles Immediately Before or During Absinthe Excitation.

In this series, whilst a tracing of a series of normal fits was being taken, both cerebral peduncles were divided; this resulted in complete arrest of the fits, but slight alteration in the respiratory rhythm could be obtained on injecting more absinthe. Thus, in one case, three minims of absinthe were injected, which was followed by irregular breathing for a few seconds, then a series of shallow respirations, followed by a deep inspiration. Four minutes afterwards the breathing became very deep, and a second dose of absinthe had a slight quickening effect. Death one hour from commencement. No tail spasm phenomena. In some cases, however, the latter phenomena were present.

Series B.—Removal of Left Hemisphere, and, After Recovery, Removal of the Right Hemisphere and Immediate Absinthe Excitation.

I have performed this experiment many times, and the results have been uniform, namely, the arrest of the typical fits.

Examples.—Cat 6. Fifty-eight days after the removal of the left hemisphere, the animal having completely recovered, the remaining hemisphere was divided, and three minims absinthe injected. There was a slight respiratory response; slight prolonged muscular contraction on the right side, and none upon the left. That is to say, the contraction corresponds to the side from which, fifty-eight days previously, the hemisphere was removed.

Cat 23.—Cat in excellent condition seventeen days after removal of left hemisphere. Divided remaining hemisphere, and injected repeated doses, after intervals; there was a slight effect upon respiration, but none upon the muscle lever.

Cat 3B.—Cat in similar condition to the preceding, and seventeen days after the first operation. Divided right hemisphere, and injected three minims absinthe. I obtained upon the right side a few muscular contractions, but there was no respiratory fit to correspond. After a further dose, however, there was an undoubted fit, which was shown by a slight prolonged contraction upon both sides. Post mortem it was found that the right hemisphere had not been completely divided, a small tag of crus remaining uncut.

Cat 5B.—Cat in excellent condition; left hemisphere removed thirteen days previously. Having obtained a well-marked series of bilateral fits, fig. 48, the right hemisphere was divided; as seen in the tracing 51, bilateral movements were produced, which took the place of the bilateral well-marked fits. The explosions take place at regular intervals, are related to the absinthe injected, and are marked by all three levers. They differ from the ordinary fits in the absence of clonus.

Cat 6B.—Animal perfectly healthy eighty-two days after the operation. Obtained

bilateral fits, then divided right hemisphere. Fits stopped, but a series of reflex convulsions were elicited by striking the ears, especially the right one; the absinthe had undoubtedly increased their reflex effects.

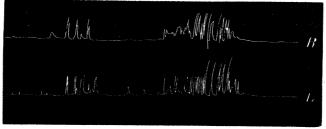
Cat 8B.—Animal recovered nine days after first operation. Divided remaining hemisphere, and gave two minims absinthe. Scarcely any change, although the animal remained alive for a very long period.

Cat 10B.—Animal completely recovered seventy-five days after first operation. Divided remaining hemisphere, and injected absinthe. After one minute there was a very slight and prolonged elevation of the levers on both sides, accompanied by the tail phenomenon; after the lapse of several minutes the asphyxial spasms commenced, and were more marked upon the right side than upon the left.

Series C.—Removal of both Hemispheres, and upon the following day Absinthe Excitations.

I succeeded in obtaining one very remarkable tracing—fig. 8. Immediately after the injection of four minims of absinthe, the three levers responded to an explosion lasting about twelve seconds, and this was succeeded after a short interval by a second





Both hemispheres removed, and, on following day, absinthe excitation.

manifestation. As the tracing shows, the fit is manifested by clonic contractions, and in the second fit by a slight tonus in addition. The rhythm is slower and more irregular than that seen when the cortex is present.

Summary.—Immediate removal of the hemisphere arrests the fits; a slight respiratory response can, however, be elicited by absinthe.

Removal of second hemisphere after recovery from removal of first, and absinthe excitation. There are respiratory and muscular responses; the latter consist of a few shallow contractions occurring at regular intervals, and equal on both sides. In one case the contraction was most marked upon the side corresponding to the hemisphere which was first removed.

Removal of both hemispheres, and stimulation upon the second day, was followed in one case by two fits made up of a series of contractions following one another fairly rapidly, but not so rapidly as in the clonus when the hemisphere is present. Thus a

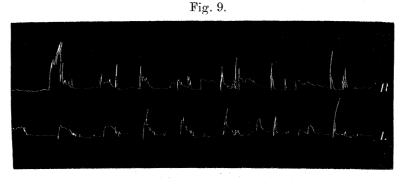
slight prolonged tonic contraction, a series of single or double contractions, or a slow clonic fit may be obtained by absinthe in the absence of the hemisphere.

Removal of both Motor Areas.

A tracing taken from a cat in which the left motor area had been removed on August 23rd, 1893, and the right one on September 6th, showed, after absinthe was injected immediately after the last operation, a regular series of responses. The fits were almost the same upon both sides, and were both clonic and tonic; the rhythm of the clonus is, however, not nearly so rapid as when the cortex is intact. A tracing from a second case exhibited much the same.

Removal of the Cerebellum, and Immediate Absinthe Excitation.

The operation being a very severe one, it is difficult to obtain tracings. In one of the most successful experiments, and of which unfortunately I do not possess a graphic record, four minims of absinthe were injected, and were followed by a long series of very typical fits; towards death the fits diminished, breathing became deep, slow, and regular. The cerebellum had been very completely removed.



Cerebellum removed, immediate absinthe excitation.

Fig. 9 is a tracing from another case. There is a regular series of small fits, fairly equal upon both sides. Clonus and tonus is present.

Removal of Right Lobe of the Cerebellum.

The right lobe of the cerebellum was removed on August 30th, and the experiment made September 4th. The animal had made a good recovery. The tracing showed a beautiful series of typical rhythmic clonic fits, with slight tonus; the fits were quite similar on both sides.

Removal of Left Hemisphere and Left Lobe of the Cerebellum.

A tracing shows fits upon the left side, and corresponding slight contractions upon the right side.

Removal of Left Hemisphere and Right Lobe of the Cerebellum.

In one case where these operations were made, and absinthe given, a few well marked clonic fits occurred upon the *left side*, whilst the movements of the other side were slight.

Removal of Right Lobe of the Cerebellum and the Left Hemisphere.

Series A.—Three tracings were obtained from cases in which the right lobe of the cerebellum and the left hemisphere were removed, and absinthe injected immediately. In all three the effects of shock are considerable; in two cases the slight fits present are almost confined to the left side. In a third case, there were two well-marked typical clonic fits, that on the left side being the most powerful, that on the right side possessing more tonus; the tracing was quite similar to that which would be obtained if the left hemisphere alone were removed.

Series B.—In this series the right lobe of the cerebellum was removed some days or weeks before the removal of the left hemisphere, and immediate absinthe excitation.

One of the tracings obtained so strongly resembles fig. 7 that it is unnecessary to reproduce it. Fig. 7, it will be remembered, was obtained from a cat in which the left hemisphere was removed, and absinthe immediately given.

Summary.—Removal of the whole cerebellum does not stop the fits, nor impart to them any special character.

Removal of one lobe of the cerebellum appears to have no effect upon the fits as measured by the absinthe method in the cat. Where it is combined with removal of the left hemisphere, the fits are similar to those seen when that hemisphere alone is removed.

Hemisection of the Mesencephalon at about the Level of the IIIrd Nerves.

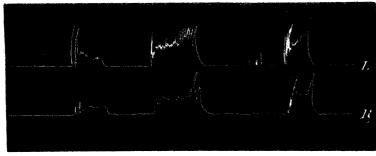
Two successful tracings were made from the cats described in the previous sections, and which had made a complete recovery.

Fig. 10 shows a typical series of clonic fits upon the left side, whilst the corresponding ones upon the right side show little clonus; the initial fit is only present upon the left side.

Summary.—The fits resulting from division of the left crus cerebri, in the region

of the corpora quadrigemina, are similar to those obtained when the left hemisphere is removed.

Fig. 10.



Hemisection of mesencephalon on left side.

Fig. 11.



Left hemisphere removed, and, after recovery, hemisection of the cervical spinal cord on right side.

Fig. 12.



Left hemisphere removed, and, after recovery, hemisection of the cervical spinal cord upon the left side.

Removal of Left Hemisphere, and Subsequent Section of the Right and Left Halves of the Cervical Spinal Cord.

Two tracings were obtained in these cases, which have the merit of representing very accurately, when placed side by side, the tracing which one would expect to get, upon the right and left side, if the hemisphere alone were removed.

Fig. 11. Cat 20B. Left hemisphere removed, June 13th, complete recovery; June 28, divided cervical spinal cord as high up upon the right side as possible, and injected absinthe. The result, as seen in the figure, was a long series of typical normal clonic and tonic fits, limited entirely to the left side.

Fig. 12. Cat, 26B. Left hemisphere removed, July 13th, recovery; June 15th,

divided upper cervical cord upon the left side. The result is right-sided fits alone, which are characteristic of the right side when the left hemisphere has been removed, i.e., mainly tonus.

Summary.—In cats with one hemisphere, section of either side of the cord abolishes conduction on the side of section. The tracings combined are similar to those obtained when the left hemisphere is removed.

Complete Section of Cord.

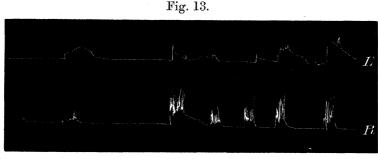
Absinthe stimulation immediately after the operation gives rise to no fits in the There are, however, facial movements corresponding to the fits.

The injection of absinthe after recovery from complete section has not been tried.

Hemisection of the Upper Cervical Spinal Cord, and Absinthe Stimulation after Recovery.

Three tracings were made.

In one animal, in which the hemisection was made on July 18th, and absinthe given July 24th, the fits were unilateral. This corresponded with the fact that the animal at the time of injection had not regained the use of the limbs on the side of lesion. Different, however, from this result are those obtained from animals in which the recovery from the paralysis was considerable. Fig. 13 is a tracing from a



Hemisection of the cervical spinal cord on left side, and, after recovery, absinthe stimulation.

cat in which hemisection was made on the left side, on July 17th, and absinthe given July 26th. The fits upon the right side are typical; on the left side, however, there are very powerful corresponding responses to the absinthe stimulation, but they are tonic rather than clonic.

Summary.—Hemisection of the cord, and immediate absinthe stimulation, stops conduction upon its side. In cats which have partially recovered from the effects of the hemisection, absinthe produces a response upon the side which was divided.

PART IV.—CONCLUSIONS.

The necessity of combining the experimental and anatomical methods of research has never perhaps been so strikingly illustrated as in the nervous system. Its anatomical investigation has yielded a succession of new results, in the foremost rank of which stand those obtained by the methods of the two Italians, Marchi and Golgi. The success attending the latter method, in the hands of Ramón y Cajal, has furnished us with a trustworthy plan, which at once enables us better to grasp the working of the nervous system, and to experiment with improved chances of success in a field which, to use Ramón y Cajal's words, "in spite of the little happy success that still attends the enquirer, must yet be regarded by the anatomist, physiologist, and pathologist as one of the least known."

The morphological deductions of Gaskell, and the results obtained by Professors Gotch and Horsley with the galvanometer and electrometer have, owing to their success, also conduced to new work; and the few fresh facts which may have come out in the preceding pages are the direct outcome of questions raised by the last two observers.

Anatomical Results.

The more our anatomical knowledge of the nervous system increases, the more uniform does the ground plan become. CAJAL expresses the difference between the brain and spinal cord by saying "Das Rückenmark stellt ein Gehirn nur umgekehrt vor, d. h. ein Gehirn, in dem die weisse Substanz nicht central liegt, sondern die peripheren Schichten einnimmt." GASKELL has shown that the upper segments of the bulbo-spinal system possess an arrangement of grey matter and of nerves essentially similar to that in the cord. According to this observer the oculo-motor may be regarded as the first segmental nerve, whilst the descending root of the Vth belongs really to the first or second bulbo-spinal segments. My experiments have shown that I never fail to obtain descending degeneration of the descending root, when I injure the Sylvian grey matter in the neighbourhood of the nuclei of the oculo-motor. They further show that these fibres pass out of the bulb without interruption, so therefore, they, in all probability, correspond to efferent root fibres, and are the axis cylinder processes of motor cells in the Sylvian grey matter, and belong to the highest segments of the bulb. In no other case have I seen evidence that the fibres of the remaining degenerate tracts which I have described, internuncial or pyramidal, pass out into the nerve roots, a fact which accords with the results obtained by the Golgi method.

The great bulk of the anterior and lateral columns consists of internuncial fibres. Golgi and R. y Cajal have demonstrated them taking origin in cells in the grey matter, then passing out into the columns, descending, and finally again turning into

the grey matter and forming an end ramification. Some fibres cross over in the anterior commissure. The researches of R. v Cajal, Kölliker, and others show, according to Cajal, that the commissural fibres are the axis cylinder processes of cells in the grey substance—the "commissural cells," and also "collaterals" of the antero-lateral fibres which run downwards. They terminate in a similar manner to the vertically coursing fibres. Thus segments upon the same and upon opposite sides are connected together. As the nervous system is traced downwards through the animal series, the more marked and independent of the pyramidal becomes the internuncial system.

When a hemisection is made in the cord the internuncial and commissural fibres are cut across; a large number degenerate downwards, others upwards. Of those which descend some soon turn into the grey matter, others can be followed for long distances. Some degenerate fibres can be seen passing in the anterior commissure, and through the grey substance to the opposite side, to turn down in the anterolateral columns. These may be the source of the "recrossed" fibres of Sherrington, seen in hemisections of the cord. As I have already pointed out, the embryological, anatomical, and pathological methods have, in the hands of numerous observers, tended to show that a similar system was to be met with in the higher bulbo-spinal segments; by the Marchi method, I have been enabled to demonstrate the descending internuncial and commissural fibres from the level of the oculo-motor segment Briefly stated, the evidence shows that large medullated fibres, taking their origin from the antero-lateral Sylvian grey matter, pass downwards both upon the same side, and cross to the opposite side. Of those which pass down upon the same side a notable group are those which lie to the inner side in the posterior longitudinal The others cross in Meynert's fountain-like decussation. It seems not unreasonable therefore to suppose that this decussation is homologous to the commissural and arcuate decussation of lower segments. Not all Meynert's fibres decussate to run down in the antero-lateral columnar tract; there is evidence that a very few may run down in the corresponding tract on the same side.

The lateral tract of the oculo-motor segment I have shown also to be largely composed of fibres which have decussated, and which have originated, in all probability, from an area close to that giving rise to the former columns.

Thus, I may conclude, that the hemisection in the highest segment of the bulbospinal system, agrees essentially with that in the spinal cord. The variation is the striking decussation.

Having described these "internuncial" systems, I have no direct evidence of my own to show that they connect certain definite nuclei; but, reasoning from analogy, it seems most probable that they do, and that thus ganglion cells of the very important quadrigeminal region are brought into relationship with important nuclei both upon the same and upon the opposite side.

The Pyramidal System.

R. Y CAJAL thinks that the corpus callosum corresponds to the anterior commissure of the cord, and contains, amongst other fibres, collaterals and bifurcated branches derived from the pyramidal fibres, as well as direct axis cylinder processes from pyramidal cells. He thinks that these fibres connect different cell layers, and Having given off the callosal collaterals, and different regions of the cortex. descending directly, the pyramidal fibres pass to the bulbo-spinal segments, and terminate in end ramifications, in what Professors Gotch and Horsley term "fields of conjunction," in the grey matter. Cajal briefly explains the nerve stream in the pyramidal system by saying, that cellulipetal impulses arouse the pyramidal cells, and cellulifugal leave them. Professors Gotch and Horsley draw attention to the fact that in the cord the pyramidal tract runs with the afferent fibres rather than with the efferent. In the higher segments the same association may be noted, to wit, the fillet, superior cerebellar, peduncle, and pyramid. The anatomical plan shows that not only is there juxtaposition of the tracts of the posterior roots and the pyramids, but that, as in the case of the latter, cellulipetal impulses arouse the posterior ganglion cells, and cellulifugal leave them to impinge on the executive system in the field of conjunction. Thus, pyramids and posterior columns alike convey directive impulses to the executive centres of the bulbo-spinal system.

From the evolutionary, and from that standpoint which makes Cajal say "Das Rückenmark stellt ein Gehirn nur umgekehrt vor," perhaps the most comprehensive view of the pyramidal system is that which regards it as a specialized portion of the internuncial system, which becomes more strongly represented as the animal scale is ascended. Or, expressed differently, in proportion as external sensations tend to concentrate in the fore brain, and cease to be merely reflected through the bulbo-spinal centres.

The development of the pyramidal tract varies in different animals. Thus, the hind limbs of the rabbit may receive a very small supply of pyramidal fibres, whilst in smaller rodents, which use their arms and legs for prehension and feeding, the fibres are well marked. The pyramidal tracts of the monkey and of man are much greater than those of the cat or dog. I have shown in the cat that not all the pyramidal fibres pass to the opposite side of the decussation, but that some pass through the grey matter to the lateral tract of the same side. Muratoff has recently shown the same in the dog, and still more recently Dr. Mellus in the monkey. In the cat and dog the number of fibres remaining on the same side appear few; in the monkey they are numerous, but there is not at present sufficient evidence to show whether the proportion between crossed and uncrossed fibres is approximately the same in the animals, or whether the bilateral distribution in the monkey is in excess of the other animals. There is no Turck's tract in the cat, dog, or monkey, man appearing to stand alone in this respect, and not without question.

As I have already mentioned in the foregoing pages, MURATOFF very recently suggested that the place of the direct anterior pyramidal tract is taken in the lower animals by fibres which, for convenience, I will term direct lateral pyramidal fibres. A similar comparison had suggested itself to me. I have commented upon the variability of the direct pyramidal tract in man, showing that in well-marked but limited cortical lesions it might be absent; on the other hand, that both crossed tracts might be degenerate, but without anterior or unilateral lesions. From the evidence I was inclined to doubt the significance at present attached to Türck's column, namely, that it is truly cortical. I have, however, not succeeded in showing that in the newborn dog or cat there exists a non-medullated tract in the anterior column similar to that in man; my experiments are not, however, complete on this point. I had hoped to find such a non-medulated tract in an animal in which I knew there was no direct anterior cortical tract, and by finding it to be able to directly show reason for contesting the pyramidal nature of the tract in man. I can offer, therefore, nothing which negatives directly the results obtained by Flechsic, however closely my anterior columnar fibres may simulate a direct pyramid. If, on the other hand, the suggestion proves correct that the direct lateral pyramidal fibres are the equivalents of the direct anterior, then the irregularities of Flechsig-Türck's pyramidal columns can be more readily understood. It may be found at the bifurcation that, as usual, the major portion of the pyramid passes to the opposite side, that some fibres remain, and run down in the anterior column, or take the third alternative and pass back to the lateral tract of the same side. Should an anterior direct pyramidal tract exist, it is probable that its fibres will be found to pass back through the grey matter to reach their destination, running previously, perhaps, for a short distance in the lateral tract.

From the above statements it will appear evident that the cellulifugal impulses from the pyramidal cells are not confined rigidly to one crossed pyramidal tract, but that there are in addition channels for the passage of impulses to the opposite cortex and to the same side of the cord. This is a method of distribution which again recalls that of the posterior ganglionic. In the upper bulbo-spinal segments a great deal remains to be done to show the connection of the pyramids with the cranial nerve centres. As in the cord, the pyramid is situated at a distance from the motor grey matter. In the mesencephalon, pons, and medulla, I have convinced myself by the Marchi method that fibres are constantly leaving the pyramid and turning back in the raphé, and it may be yet shown that these fibres really represent a decussation, and that they are passing back to gain the field of conjunction of the motor nuclei on either side. Another system of fibres are those which I mentioned leaving the outer angle of the crusta, as well as those passing directly out of the internal capsule, and which come into such close relationship with the geniculate body. This system of fibres passes to the quadrigeminal on the same side, and over the roof of the aqueduct to that of the opposite side. It is a collateral system which, like the main mass, appears to have a bilateral distribution.

Seat of Origin and Conduction of the Impulses in Epilepsy.

According to Cajal we may picture the reflex act as aroused by impulses which travel by the posterior ganglionic fibre, are distributed amongst the separate branches which this fibre breaks up into, and finally impinge on the motor cells by means of the end or contact ramifications which each branch forms in the vicinity of the motor cells. He puts forward the end or contact plate theory against the theory of anastomosis of von Kölliker and Waldeyer. It is thus, he adds, that we can understand why a weak stimulus only awakes a reflex in a limited number of muscles, whilst stronger stimuli produce widespread and complicated actions. In the former case the impulses pass out by the first-formed collaterals and stimulate a few motor root cells; in the latter case they spread along the ascending and descending branches, and throughout all the collaterals, and act upon a much larger group of motor cells.

This picture of the reflex act seems the most complete that has yet been offered, and the one which explains the greater number of motor phenomena; it is the one upon which I am enabled to interpret the results obtained by absinthe excitation.

In their work upon the Mammalian nervous system, Professors Gotch and Horsley discuss at great length the question of bilaterality. They show that "it is possible to obtain strictly unilateral effects in both the spinal cord and sciatic nerve with complete excitation of both cortex cerebri and corona radiata." They conclude that, "as far as the cortical efferent representation of the lower limb in the cat and monkey is concerned, the normal condition is that of unilaterality." That, when bilaterality is witnessed, it is brought about by agencies which may be supposed to act upon other portions of the central nervous system, and they emphasise, in more than one place, the opposite cortex, the cerebellum, and basal ganglia. "An adequate stimulus, which completely discharges the cortex at one given focus of representation of one limb, produces movement in that limb only, and none in the limb of the same side." Finally that, "when (bilateral) movements of both limbs follow excitation of one hemisphere, after the excitable cortex of the opposite hemisphere has been thrown out of gear by ablation, division of the commissures, &c., &c., the movements of the limb on the side opposite to the cortex excited is the complete cortical effect of tonic, followed by clonic contractions, whereas the movement of the limb on the same side as that of the cortex excited is only a tonic contraction."

Now I think that these pregnant observations are in accord with Cajal's enunciation of the reflex, and that the raising of the question of bilaterality only, or unilaterality only, is unnecessary.

The "adequate stimulus" applied to the cortex by an experienced hand by means of a delicate pair of electrodes unquestionably evokes a unilateral effect.

We know from what has been shown above, in connection with the distribution of the pyramid, that the greater path of conduction leads to the opposite side.

It would be hardly necessary to suppose in this experiment that the electrodes only affected pyramidal cells which possessed axis cylinders, which passed to the opposite side of the cord to their destination, without ever branching or ever giving a collateral. From what we now know of the course and branching of the pyramidal fibre, it is more rational to suppose that the impulses, as in the case of the posterior root fibre mentioned above, pass by the most direct channels, which are those which conduct to the opposite side, as measured anatomically, galvanometrically, or graphically. For both Professors Gotch and Horsley show, working with more than the "adequate stimulus." a difference of bilateral effect, as tested with the galvanometer, in the proportion of 87 to 28, in the halves of the cord (corona radiata stimulated, the opposite hemisphere being absent), or 16 to 2.5 in the case of the sciatics; and in the case of the graphic record of a muscle, tonus + clonus upon the opposite side, tonus on the same side.

If the stimulus is increased, the effect is bilateral, or universal, producing epilepsy. It would be difficult to say which is the more frequently used of the alternative routes, the callosal or the direct pyramidal. We know, however, that in the absence of one hemisphere, or of one motor area, the direct pyramidal path is readily used. It, moreover, appears more probable that this should be the next easiest path.

It has no break in it, whilst that by the corpus callosum has, necessitating, as the experiments of Gotch and Horsley tend to show, delay at the junction.

In my own experiments with absinthe, I have not noticed a delay upon the opposite side when one hemisphere was removed, and the quantity of absinthe was sufficient to arouse well-marked fits.

It is unnecessary for me to recapitulate the conclusions of the numerous observers who have worked upon the subject of electrical excitation of the nervous system. These are to be found in Professors Gotch and Horsley's work, but, as they themselves say, the opinion of most authors is that bilaterality does exist.

Concerning the *cerebellum*, and the share it may take in the production of bilaterality, or in the production of muscular movements—in man, the superior cerebellar peduncle is of very great size, in the cat it is not very large; it is centrifugal from the cerebellum.

I have not observed in any of my cerebral ablation experiments fibres going to the cerebellum from the brain, unless it should be some fibres derived from the pyramid.

The vast majority of the fibres which leave the cerebellum, therefore, pass towards the opposite hemisphere; I have no data at hand yet to say how many fibres may pass to the bulbo-spinal centres, and for reasons before stated, I doubt MARCHI'S conclusions.

It seems rational to suppose that the cerebellum, receiving as it does external impressions, should reflect some to the bulbo-spinal centres, as well as to the brain, so I conclude, therefore, that when I administer absinthe, I also excite the cerebellum, just as I excite every other bulbo-spinal centre.

But I have shown that, in the absence of the cerebellum, typical fits may be observed; nor can I say, in the very numerous cases in which I have removed one cerebral lobe, or one cerebral lobe and the opposite hemisphere, that I have obtained a characteristic tracing, such as I could immediately say was due to the loss of cerebellar substance. I therefore see no sufficient reason for assuming that the cerebellum may take an unusual share in the production of a fit.

In the case of the *lenticular* and *caudate nuclei*, and the *optic thalamus*, I know of no anatomical paths which connect them to the bulbo-spinal centres. Whether these ganglia are removed upon one side in the case of a complete removal of a hemisphere, or whether the motor area alone is removed, the fit is so slightly altered that I should hardly be justified in attributing the slight weakening effect to the direct want of action of these organs.

Summary of the Results obtained by Absinthe, and the Conclusions derived therefrom.

Absinthe acting upon the bulbo-spinal centres (including the cerebellum) alone, can produce a series of clonic fits, differing from the cortical in the slower rhythm of the contractions.

MAGNAN,* with the same agent, came to the same conclusions.

Professor Horsley repeats in the Croonian Lecture a former observation, namely, that complete section of the cord at the 8th dorsal vertebra prevents the appearance of the characteristic convulsions in the lower limbs.

I have in the preceding pages also recorded that, with complete section in the upper cervical region, there are no fits; but, on the other hand, it must be remembered that I have as yet no data to show that if the animal recovered contractions might not be elicited. For whilst an immediate hemisection prevents fits upon that side, it is otherwise if the operation is performed days or weeks before the absinthe injection.

Professors Horsley and Gotch state that a strong stimulus applied to the lateral column of the divided cord so arouses the centres that they continue to discharge after the stimulus has ceased. The injection of strychnine, it is well known, increases the excitability of the bulbo-spinal centres to a remarkable degree. We have already pointed out that with absinthe the reflex excitability is increased at certain stages. I therefore conclude that absinthe may possibly arouse a spinal epilepsy.

Immediate hemisection of the cord prevents the absinthe fit; but, if recovery is allowed to take place, a modified fit results upon the side of the lesion, in spite of the fact that the direct lateral and crossed pyramidal tracts are completely degenerate, as well as the internuncial fibres in the anterior and lateral columns.

To explain the bilateral result after recovery, and after such extensive degeneration, we may assume that the impulses which travel down the intact side and arrive in the

^{*} Magnan, 'Recherches sur les Centres Nerveux,' Paris, 1876.

field of conjunction, stimulate the motor cells upon the opposite side as well as upon their own side. The commissural fibres also probably aid in this. But, in as much as the fits are abolished after immediate section, we must assume that, using absinthe, the power of transmitting impulses from one side of the grey matter to the opposite side requires a short time for its development.

Professors Gotch and Horsley obtained with intense stimuli a slight response on the side of immediate section, but with ordinary stimuli no effect. They explain it likewise upon the supposition of a heightened reflex.

I may here point out the phenomenon of the increased reflex after hemisections observed by Brown-Séquard.

When a motor area or one hemisphere is removed, or a complete hemisection made in the quadrigeminal region, there are bilateral fits, in spite of the fact that the opposite pyramid is completely degenerate.

The fits are modified upon the side opposite to the lesion, the clonus being less marked; the first fit may be absent or very small.

We have shown reasons for explaining these phenomena by the presence of direct lateral pyramidal fibres derived from the sound pyramid, for, if after a hemisphere is removed and degeneration has taken place in the opposite pyramid, a hemisection is made on the side of the degenerate pyramid, it instantly arrests the fits upon that side.

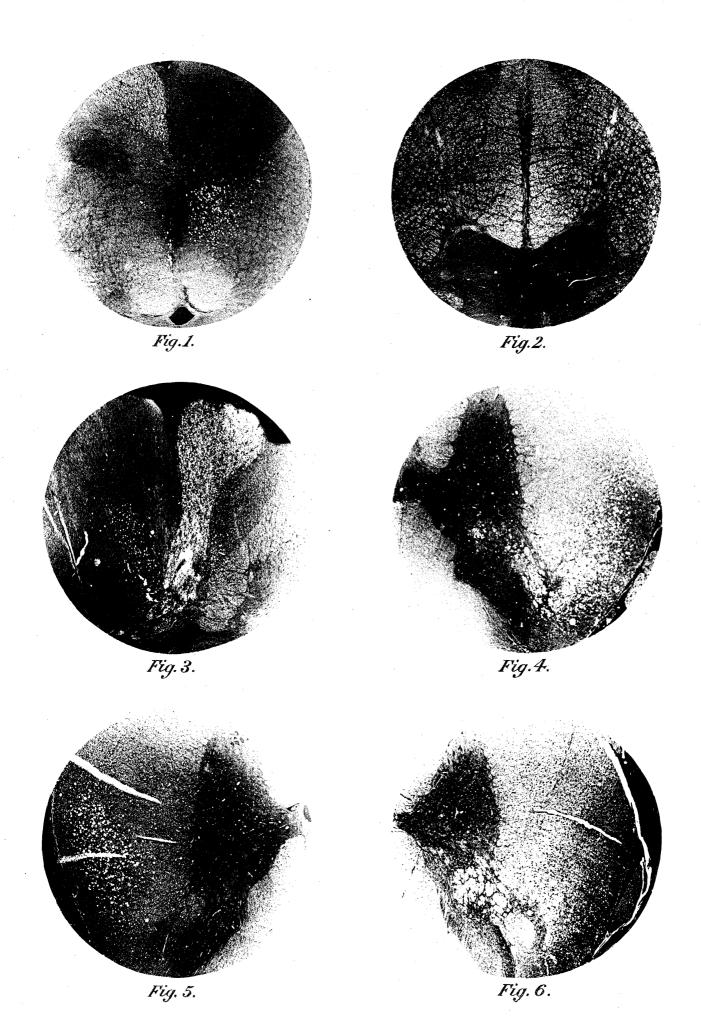
I therefore conclude that the maximal effect of absinthe is produced upon the cells of the motor area, and that the impulses generated there are distributed by the pyramidal system in the way described.

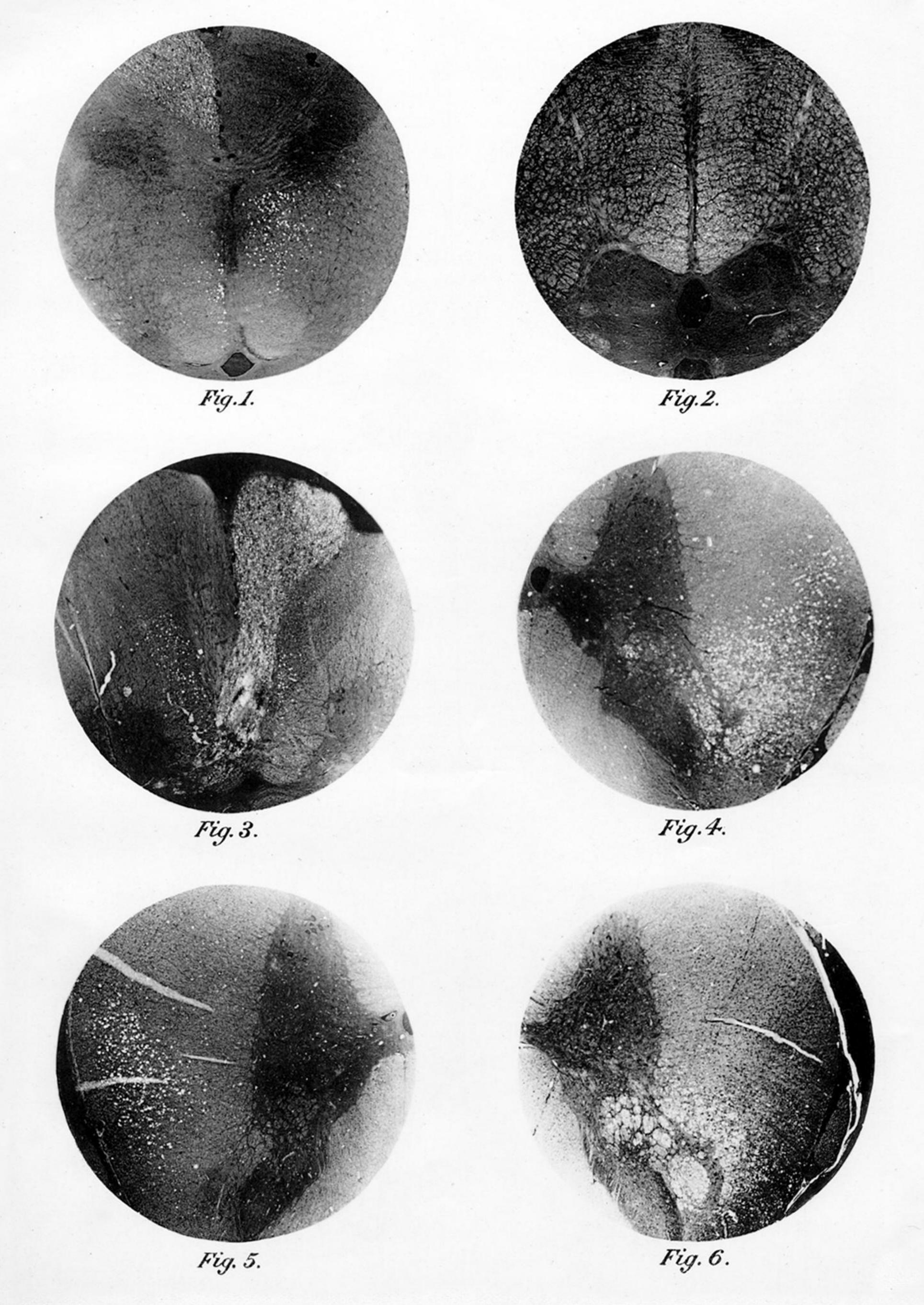
But I will not state yet that this is the sole explanation in the cat, seeing that the direct lateral pyramidal tract is so very small.

DESCRIPTION OF PLATE 3.

- Fig. 1. Section through the medulla at level of nucleus of the 12th. The degenerate left pyramidal tract is seen, as well as the position of the degenerate antero lateral and anterior (posterior longitudinal bundle) columnar fibres. Cat, in which left hemisphere was removed.
- Fig. 2. The same level as the preceding. Motor area of cortex only removed.

 There are no degenerate antero-lateral or anterior columnar fibres.
- Fig. 3. Commencement of the pyramidal decussation. The *left* degenerate pyramid is seen (right side in figure) and the relative positions of the antero-lateral and anterior columnar fibres.
- Fig. 4. Upper cervical region. The combined area of degeneration formed by the crossed pyramidal tract posteriorly, and the lateral columnar fibres anteriorly, is seen.
- Fig. 5. Same level. The degenerate lateral columnar fibres only.
- Fig. 6. Same level. The degenerate crossed pyramidal tract only.





DESCRIPTION OF PLATE 3.

- Fig. 1. Section through the medulla at level of nucleus of the 12th. The degenerate left pyramidal tract is seen, as well as the position of the degenerate antero lateral and anterior (posterior longitudinal bundle) columnar fibres. Cat, in which left hemisphere was removed.
- Fig. 2. The same level as the preceding. Motor area of cortex only removed.

 There are no degenerate antero-lateral or anterior columnar fibres.
- Fig. 3. Commencement of the pyramidal decussation. The left degenerate pyramid is seen (right side in figure) and the relative positions of the antero-lateral and anterior columnar fibres.
- Fig. 4. Upper cervical region. The combined area of degeneration formed by the crossed pyramidal tract posteriorly, and the lateral columnar fibres anteriorly, is seen.
- Fig. 5. Same level. The degenerate lateral columnar fibres only.
- Fig. 6. Same level. The degenerate crossed pyramidal tract only.