XIV. *Degenerations Consequent on Experimental Lesions of the Cerebellum.**

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Communicated by Professor Victor Horsley, *F.R.S.*

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

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[Plate 14.]

Contents.

I. Introduction.

It is with much pleasure that I return my thanks to Professor Victor Horsley for placing the facilities which obtain at the Pathological Laboratory of University College, London, at my disposal for the present investigation; and Professor Rubert Boyce for bringing his large experience of the "Marchi method" to my aid in the

* Part of the expenses connected with this investigation have been defrayed by a grant from the Scientific Grants Committee of the British Medical Association.

criticism of my results, as this method of tracing the degenerated nerve fibres has been exclusively employed in the present investigation.

The discrepancies which exist between the results as obtained by MARCHI in tracing the degenerations consequent on ablation of parts of the cerebellum, and those obtained by FERRIER and TURNER after similar lesions of this organ, are sufficient reasons why I should record my experience in this connection.

I determined to employ MARCHI'S own method of tracing the degenerations consequent on ablation of parts or the whole of the cerebellum, and had conducted a large number of such investigations, before I became aware that FERRIER and TURNER had undertaken the same task, a fact which was made known to me just before these observers brought their results before the Royal Society.

FERRIER and TURNER have relied mainly on the WEIGERT or WEIGERT-PAL method of staining the tissues in their attempts to trace the degenerations which result from lesions of the cerebellum; but no contradiction of MARCHI'S results based on this method of tracing the degenerations can be accepted as conclusive, for there can be no question that the WEIGERT-PAL method cannot compare in delicacy with the MARCHI method for tracing small tracts, or the terminal ramifications of large ones. It is not surprising therefore that my results do not entirely accord with those of FERRIER and TURNER, though they do so in respect to certain points in which these observers believe MARCHI'S results to be erroneous.

I hope to be able to show further, that I have obtained certain results which do not appear to have engaged the attention of either of the observers whose results are so discrepant.

Inasmuch as very important differences may depend on the length of time that the animal is allowed to live after the operation, before the central nervous system is examined by a method whose efficacy depends on the existence of what I may, perhaps, be allowed to term the primary products of degeneration, I killed the animals at different periods after the operation, varying from one week to three months.

II. RECENT SIMILAR INVESTIGATIONS.

It would serve no useful purpose if I were to review all the previous work that has been done with a view to establishing what are the connections of the cerebellum with the rest of that great system of which it is a part, for the results obtained by MARCHI are, many of them, so entirely out of keeping with anything that has been previously found in this connection, that it seems to be best to limit myself to a consideration of his, and those of FERRIER and TURNER, which may be taken as a criticism of his results.

MARCHI* has published so many communications on the subject which now engages our attention, that it is impossible to give any detailed account of his

* MARCHI, 'Riv. Sper. d. Fren. e Med. Leg.,' Anno 12, 1886, f. 1; Anno 13, 1887, f. 4; Anno 17, 1891.

results here. All that I can do is to give some idea of what some of his chief results were. He found extensive degeneration in all the peduncles of the same side, after removal of half of the cerebellum, and very little, if any, in the peduncles of the opposite side, from which he infers that none of the peduncles contain commissural fibres connecting the two halves of the organ. The degenerated fibres in the superior peduncle were traced to the tegmental nucleus of both sides, and some as far as the optic thalamus. There was complete degeneration of the middle peduncle up to the raphé. The degenerated fibres from this source were found to pass among the pyramidal fibres of both sides, and among the fibres of the fillet and posterior longitudinal bundle, mainly of the same side as the cerebellar lesion. Degenerated fibres were traced in the fillet and posterior longitudinal bundles (most marked on the side of the lesion) up to the corpora quadrigemina and down to a tract at the periphery of the antero-lateral region of the spinal cord. A bundle of degenerated fibres was also traced to the pyramidal tract up to the corpora quadrigemina, and probably also the corpus striatum, chiefly on the side of the lesion, and a few were traced into the spinal cord. There was atrophy and degeneration of the grey matter of the pons on the side of the lesion. The degeneration in the inferior peduncle involved mainly its inner and outer parts. A small bundle passed with the inner arched fibres, across the raphé, to the opposite inferior olive, which was found completely atrophied. Other degenerated fibres were traced from the restiform body to the fillet and posterior longitudinal bundle of the same side, from which they pass to the antero-lateral region of the spinal cord, and some of them down the pyramidal tract. Degenerated fibres were also traced to the roots of all the cranial nerves, the ascending root of the fifth, the striæ medullares, and the anterior roots of the spinal nerves. These degenerations were most marked on the side of the lesion, but also existed on the opposite side, the degenerated fibres to the cranial nerves reaching them by way of the posterior longitudinal bundles, and those to the spinal nerves by the descending antero-lateral tract of the spinal cord.

Removal of half of the middle lobe of the cerebellum resulted in only slight degeneration of the superior peduncle, all the degenerated fibres passing to the tegmental nucleus of the opposite side. The degeneration of the middle peduncle was most marked in the upper third of the pons, only a small amount being present in the lower two-thirds. That of the inferior peduncle occupied the outer and lateral part of the restiform body, a few fibres passing from this to the opposite side, others to the fillet and to the posterior longitudinal bundle, by which latter channel they reach the cranial nerve roots ; while other degenerated fibres were traced down the antero-lateral columns of the cord, but not down the pyramidal tract.

Ferrier and Turner* found that removal of one lateral lobe of the cerebellum, or section of the superior peduncle, demonstrated the existence of an efferent tract to

* 'Proc. Roy. Soc.,' 1893, Vol. 54, p. 476.

the opposite red nucleus and optic thalamus, and an afferent tract, which they believe to be the cerebellar termination of the antero-lateral ascending tract of GOWERS.

Lateral lobe extirpation, or section of the middle peduncle resulted in diminution of the transverse fibres of the pons on the side of the lesion, and atrophy of the cells of the nucleus pontis of the opposite side.

Lateral lobe extirpation, or section of the inferior peduncle, demonstrated an efferent tract to the opposite inferior olive, an afferent tract to the cortex, chiefly of the lateral lobe.

These observers found no degeneration in the superior, middle, or inferior cerebellar peduncles, after extirpation of the middle lobe; but this lesion resulted in degeneration and sclerosis of the tract which passes from the vermiform process to DEITER'S nucleus—the "direct sensory cerebellar tract" of EDINGER.

They were unable to confirm MARCHI'S observations on the existence of a direct efferent cerebellar tract in the spinal cord, or as to the presence of degeneration in the anterior nerve roots, mesial fillet, or posterior longitudinal bundles, after cerebellar extirpation.

In one case of lateral lobe extirpation, in which DEITER'S nucleus was injured, they obtained the marginal degeneration in the anterior column of the cord, as described by MARCHI, after cerebellar lesions; and in another case in which the tegment of the pons was injured, involving the nucleus of the lateral fillet, there was degeneration in the lateral columns of the cord.

III. OPERATIVE AND OTHER PROCEDURES.

1. *Operative Procedure.*

In all cases the back of the head and neck were first shaved, thoroughly cleansed with soap and water, and finally washed with perchloride of mercury lotion (1-1000). The skin incision adopted in all the later experiments consisted in a single longitudinal cut in the middle line of the back of the head and neck, as this was found perfectly sufficient to allow of complete exposure of the deeper parts, even where the whole cerebellum was to be removed. In my earlier experiments I was in the habit of making an additional incision transversely outward from the upper end of the longitudinal incision, either on one or both sides, according to whether a unilateral or bilateral lesion of the cerebellum was to be subsequently produced, and the skin flap was turned downward and outward on one or both sides, as the case might be. This plan, which was attended with considerably more hæmorrhage, was afterwards discarded for the simpler, and quite as effective method of exposing the deeper parts by the single incision.

Whichever of the skin incisions was employed in no way affected the subsequent course of the operation, which differed only in regard to the part of the cerebellum

removed. An incision was made along the middle line to the depth of the cervical spines; the muscles were then cut and scraped away from their attachments to the curved lines and adjacent depressions, on one or both sides, as the case might be, then working from the middle line outwards they were torn and scraped away from their attachments to the spines and arches of the upper cervical vertebræ. It is very important to work from the middle line outward, as by this means much troublesome hæmorrhage is avoided, as also obtains when very little cutting is done, tearing and scraping being relied on to free the bony parts of their soft coverings. The unavoidable loss of blood which attends the subsequent stages of the operation makes it necessary that as much hæmorrhage should be avoided as possible in the earlier stages. When I first commenced these operations I was in the habit of trephining the occipital bone, with a quarter-inch trephine, over one or other lateral lobe of the cerebellum, and then enlarging the opening, to any extent required, by means of bone forceps; but latterly the trephine was entirely discarded, the bone forceps alone being used to effect an opening into the cranial cavity. Up to this stage in the operation, perchloride of mercury lotion (1–1000) was used to wash the wound, and was supplemented from time to time, as occasion required, by hot water (about 100° F.) that had been boiled, with a view to checking any oozing; but from this point nothing but boiled normal saline solution was used to wash out the wound, and to arrest bleeding. During the removal of the bone an aseptic wax was employed to check the bleeding from the sinuses in it. The next step consisted in opening the membranes, and turning aside a flap of the dura mater which covered the part whose extirpation was intended. By means of a sharp thin-bladed knife the part to be excised was delimited from the rest of the organ, and was then carefully scooped out by means of a small sharp spoon. In scooping out the portion of cerebellum, full advantage was taken of the bony tentorium, and every care taken not to press on or injure the medulla, or the pyramidal tracts a little below this point. All the scraping was done either from below directly upwards against the bony tentorium, or downwards and outwards against the base of the posterior fossa, and never either directly downwards or inwards. Syringing out the cavity with hot normal salt solution (about 100 F.) was resorted to, both as a means of checking the bleeding and of clearing out all *débris*. The external wound was then carefully sponged with perchloride of mercury lotion (1–1000), and closed by means of aseptic horse-hair sutures, a small portion of the most dependent part of the wound being left open to allow of drainage. The wounds were dressed antiseptically, and seldom failed to unite by primary union. Only those cases which did unite by primary union were relied on for subsequent investigation of the degenerations which result from lesions of the cerebellum.

Ether was the anæsthetic employed in all cases, and the animal was kept profoundly under its influence throughout the whole course of the operation. In some instances in which the operation was so unusually severe as to suggest the

possibility that the animal might be conscious of pain when the effect of the ether had passed off, this anæsthetic was supplemented by a hypodermic injection of morphia, while the animal was still under the influence of ether.

2. *Preparation of Tissues for Microscopic Examination.*

The method adopted was that described by MARCHI, and as it has attracted so much attention, and become so generally used, it would be superfluous for me to give any detailed account of it here. Suffice it to say that by this method the tissues of the central and peripheral nervous system are hardened and stained simultaneously, and that under the combined influence of two parts of MÜLLER'S fluid, and one part of a 1 per cent. solution of osmic acid, the normal white matter becomes brown, the grey matter a very light brown or grey, while any degenerated nerve fibres, which may exist in the specimen, are stained an intense black.

3. *Examination of the Tissues.*

There are times when it is exceedingly difficult to be certain whether the black points present in a transverse section of some portion of the central nervous system in which the nerve fibres are cut across in their course, represent degenerated nerve fibres or not, therefore in the present investigation I have checked the results obtained, as seen in transverse sections, by those seen in longitudinal sections made in the direction of the course of the fibres.* When a longitudinal section of a fibre is thus seen there is no difficulty in being certain as to whether degeneration does, or does not, exist. The longitudinal sections have been made in such a way that the knife passes through as nearly as possible the same plane on the two lateral halves of the central nervous system, so as to include, in the same section, identical structures on the two sides.

IV. ABLATION OF ONE LATERAL LOBE OF THE CEREBELLUM.

It will be convenient to consider the degeneration resulting from this lesion as met with in the remaining parts of the cerebellum, and then as it is seen in the peduncles, taking the superior of these first then the middle, and then the inferior.

A. *The Remaining Parts of the Cerebellum.*

There is well-marked degeneration of fibres passing from the seat of lesion through the middle lobe across to the opposite uninjured lateral lobe. These degenerated fibres owe their existence evidently to their being severed from nerve cells on which

* MOTT, 'Journ. of Physiol.,' 1893; 'Brain,' 1895.

they depend for their nutrition, and not to any extension of inflammatory changes, consequent on the lesion, and extending from it to the remaining parts of the cerebellum. As has been already explained, any evidence of inflammatory reaction at the seat of lesion made me discard the specimen in which it was found, so that when I state that there were degenerated fibres in the remaining parts of the cerebellum, I allude to specimens in which there could be no question that the degeneration was consequent on severing the nerve fibres from the cells on which they were dependent for their nutrition.

Not only were such degenerated fibres seen in the remaining parts of the cerebellum; but some could be traced out of the otherwise healthy side of the organ, by way of its superior peduncle.

B. *The Cerebellar Peduncles.*

There is well-marked degeneration in all the peduncles on the same side as that from which the lateral lobe of the cerebellum has been removed; but, so far as I have been able to ascertain, there is no trace of degenerated nerve fibres in any of the peduncles of the opposite side, with the exception of the superior peduncle, in which there is unquestionably a bundle of degenerated fibres.

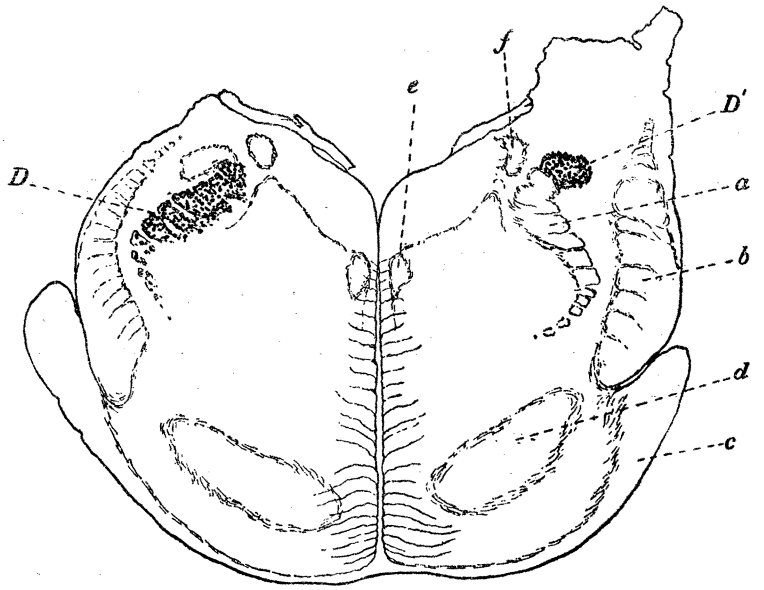
1. *The Superior Cerebellar Peduncles.*

(a.) *The Superior Peduncles on the Side of the Lesion.*—That on the same side as the cerebellar lesion contains a large number of degenerated fibres, and on transverse section these are seen to be scattered throughout the greater part of the area occupied by the peduncle, with the exception of the posterior hook-like extremity of it, which is comparatively free from any degenerated fibres (see fig. 1).

This comparative absence of degenerated nerve fibres in the hook-like extremity of the superior cerebellar peduncle, on the side of the cerebellar lesion, is significant and of great interest, with regard to certain points to be afterwards considered.

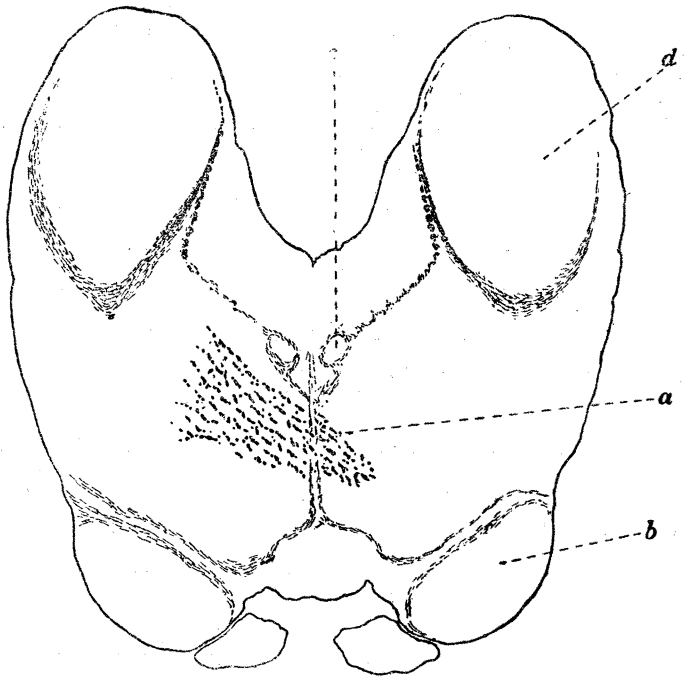
The degenerated fibres in the superior peduncle on the side of the lesion may be traced in their upward course with great ease, both in transverse and longitudinal sections. Fig. 2 (Plate 14) represents a longitudinal section through these fibres, which are seen to form a well marked strand, which courses upwards on the side of the lesion, until the region of the decussation of the superior peduncles is reached. At this point the degenerated fibres cross to the opposite side (see fig. 3). There appears to be a notable difference in the behaviour of these degenerated fibres of the superior peduncle, as they decussate in the monkey, as compared with the dog. In the latter animal they form a single band as they pass across the middle line (see fig. 4), while, in the former, the fibres separate into two bundles so as to encapsulate a portion of the *formatio reticularis* in their course (see fig. 3). But both in the monkey and in the dog these fibres appear to form a single bundle in their further upward course

Fig. 1.



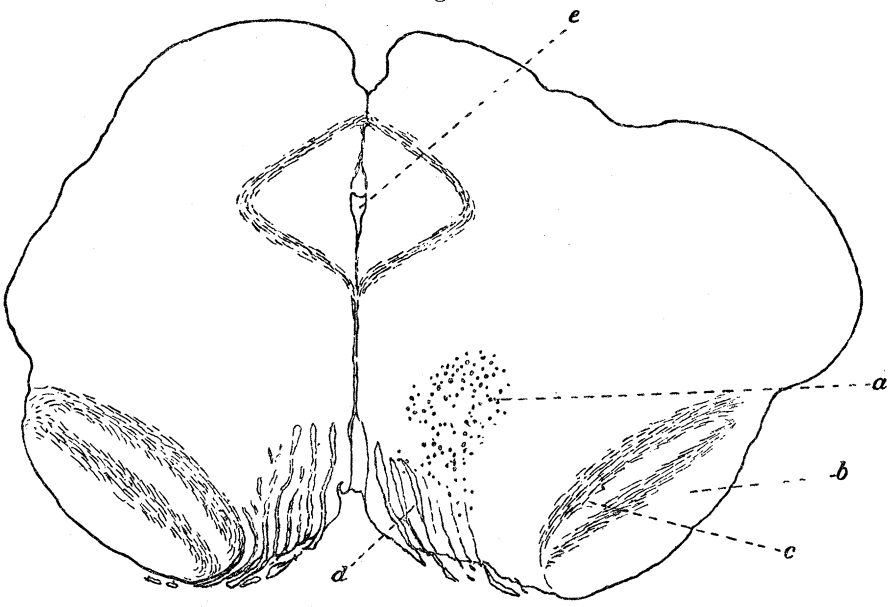
Transverse section through upper (cephalic) end of pons, showing degeneration in the superior cerebellar peduncle on the same side (D), and on the opposite side (D′) after ablation of one lateral lobe of the cerebellum. a = superior cerebellar peduncle; b = lemniscus; c = transverse fibres of the pons; d = pyramid; e = posterior longitudinal bundle; f = descending root of Vth.

Fig. 4.



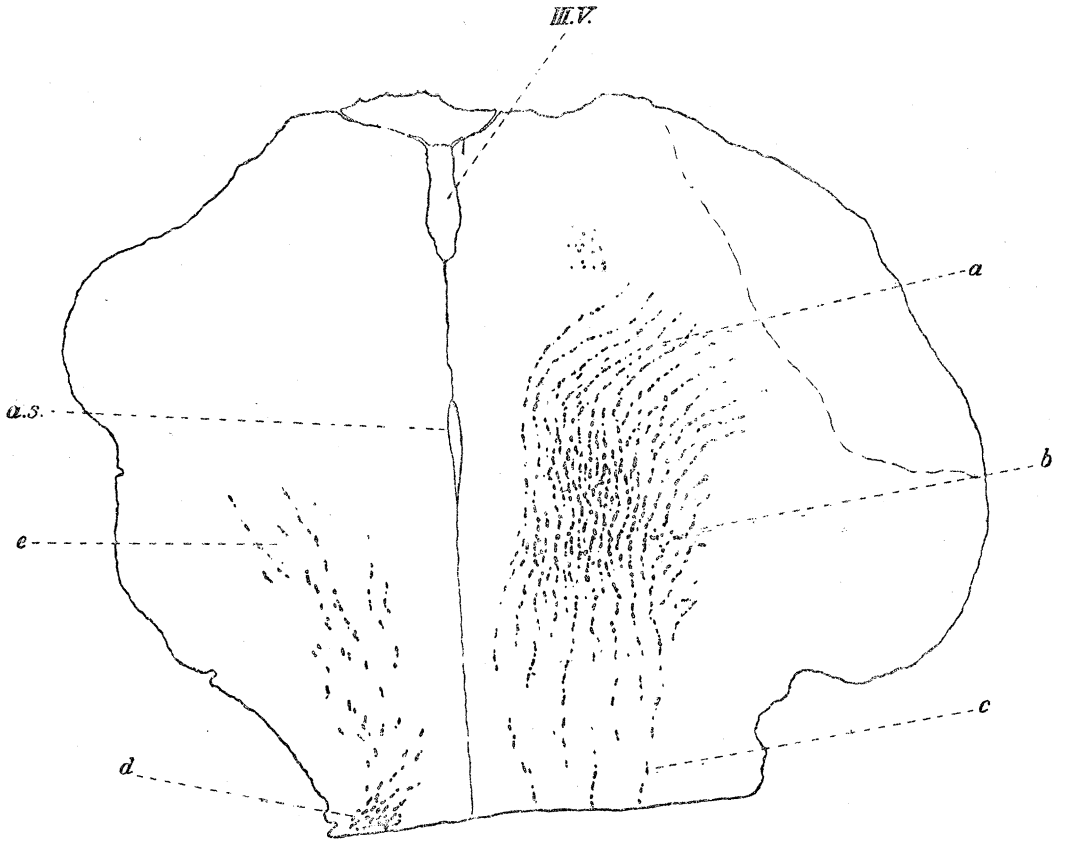
Transverse section through posterior corpora quadrigemina, showing degenerated fibres of the superior cerebellar peduncle decussating after ablation of one lateral lobe of the cerebellum. a = superior cerebellar decussation; b = pyramid; c = posterior longitudinal bundle; d = post. corp. quad.

Fig. 5.



Transverse section through crura cerebri at level of red nucleus and roots of IIIrd nerve, showing degenerated fibres of the superior cerebellar peduncle in the region of the opposite red nucleus after ablation of one lateral lobe of the cerebellum. a = degenerated fibres of superior cerebellar peduncle; b = crusta; c = substantia nigra; d = roots of IIIrd nerve; e = aqueduct of SYLVIUS.

Fig. 6.



Longitudinal section, showing the degenerated fibres of the superior peduncles after ablation of one lateral lobe of the cerebellum. a = fibres passing to optic thalamus; b = fibres which have crossed from the side of the lesion; c = uncrossed fibres from the peduncle of the intact half of the cerebellum; d = fibres on the side of the lesion which have not yet crossed; e = fibres which do not cross; $a.s.$ = aqueduct of SYLVIUS; $III.V.$ = third ventricle.

after they have crossed the middle line. As they proceed upwards they become more and more scattered, occupying a wider and wider area, but apparently diminishing in numbers until the region of the red nucleus and exit of the third nerve is reached, where the appearance presented by these fibres in transverse section is seen in fig. 5, in which the bulk of them may be seen coursing up on the outer side of the roots of the third nerve, while a few are scattered between these emergent roots.

A very large proportion of these degenerated fibres pass beyond the red nucleus (see fig. 6), and may be traced to the optic thalamus, beyond which point I have never been able to detect any degenerated fibres. There has never been the slightest evidence of any degenerated fibres passing to the cortex of the cerebral hemisphere, by way of the internal capsule, or, by any other route.

We thus see that the fibres which degenerate in the superior cerebellar peduncle, on the side from which one lateral lobe of the cerebellum has been removed, pass to the opposite side in the posterior quadrigeminal region; and that, while some apparently end in the opposite red nucleus, a large proportion have as their ultimate destination the opposite optic thalamus. But a few fibres do not cross, and these appear to end in the red nucleus on the same side as the cerebellar lesion.

(b.) *The opposite Superior Peduncle.*—When speaking of the degenerated fibres found in the remaining parts of the cerebellum after ablation of one lateral lobe, we saw that certain of these degenerated fibres passed from the intact half of the organ by way of its superior peduncle. In further tracing these fibres, as seen in transverse sections through the pons, they are found to occupy a very special position in the superior cerebellar peduncle. The very region of this peduncle, which was comparatively free from degenerated fibres on the side of the lesion, is that which is occupied by these fibres on this side; while the whole of the peduncle which showed so much degeneration on the side of the lesion, is free from degenerated fibres. In other words, the only part of the superior peduncle, on the side corresponding to the intact half of the cerebellum, which contains any degenerated fibres, is the hook-like posterior end of this structure (see fig. 1). These degenerated fibres in this superior peduncle appear to pass directly upwards to the posterior quadrigeminal region, where they become intermingled with those from the superior peduncle on the side of the lesion which have decussated. After this intermingling of the two sets of degenerated fibres it, of course, becomes impossible to trace the small bundle from the intact half of the cerebellum further as a separate tract, so that what its ultimate destination is must, for the present, remain an open question.

It seemed to me clear that these degenerated fibres in the superior cerebellar peduncle on the intact side of the cerebellum represented commissural fibres derived from the lateral lobe which had been removed, which fibres cross in the cerebellum itself to leave its intact half by the superior peduncle of that side. However, wishing to put the question to a further test, I determined to cut the cerebellum vertically in the middle line, so as to divide it into two lateral halves. It seemed to me that, if

commissural fibres did exist, which left the organ by its superior peduncles, evidence of their existence must be forthcoming after such a lesion. Nothing could be more conclusive than the actual result, for degenerated fibres were found in both superior cerebellar peduncles after this lesion; and the exact position occupied by these degenerated fibres on both sides was that occupied by the degenerated fibres in the opposite superior peduncle after ablation of one lateral lobe of the cerebellum. That is, the degeneration in both superior peduncles was limited to the posterior hook-like extremity (see fig. 7). That these are true commissural fibres, and not simply fibres which degenerate from the middle lobe of the cerebellum, in consequence of some destructive process consequent on the incision made into it, will become evident when the results of destruction of the middle lobe are considered.

2. *The Middle Cerebellar Peduncle.*

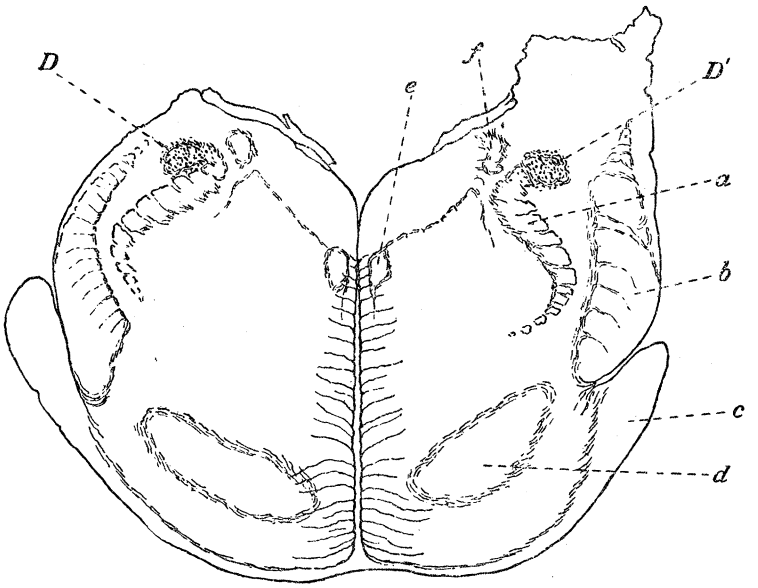
In no instance have I found any evidence of degenerated fibres leaving the cerebellum by the opposite middle peduncle after ablation of one lateral lobe of the organ. The degeneration of the middle peduncle on the side of the lesion is, however, very extensive. On transverse sections through the pons at different levels, where these fibres form the superficial transverse fibres of this organ, they may be seen coursing from the cerebellum as a well marked black band. (See fig. 8.)

The fibres continue as a single band until a point opposite the pyramids is reached, when this band bifurcates into two unequal halves (see fig. 8), much the greater number of degenerated fibres continuing their course as the superficial transverse fibres of the pons, and thus passing on the ventral side of the pyramid, while a few fibres which form the other arm at the point where the bifurcation occurs, turn more abruptly into the substance of the pons and course along the dorsal aspect of the pyramid. (See fig. 8.) Other degenerated fibres may be seen leaving the chief band which courses over the surface of the pons, and these may be traced into the pyramid which they traverse by insinuating themselves between the pyramidal bundles.

After the main band of degenerated fibres crosses the raphé, some continue their superficial course on the ventral aspect of the opposite pyramid (see fig. 8), interpolating themselves with the fibres from the opposite middle peduncle of the cerebellum, while some turn up in the substance of the pons and pass between the raphé and the opposite pyramid (see fig. 8); degenerated fibres may also be traced from this system of fibres along the dorsal aspect of the opposite pyramid (see fig. 8), and also others insinuating themselves between the bundles of the pyramid. Comparatively few degenerated fibres are seen between the pyramid and raphé on the side of the lesion. (See fig. 8.)

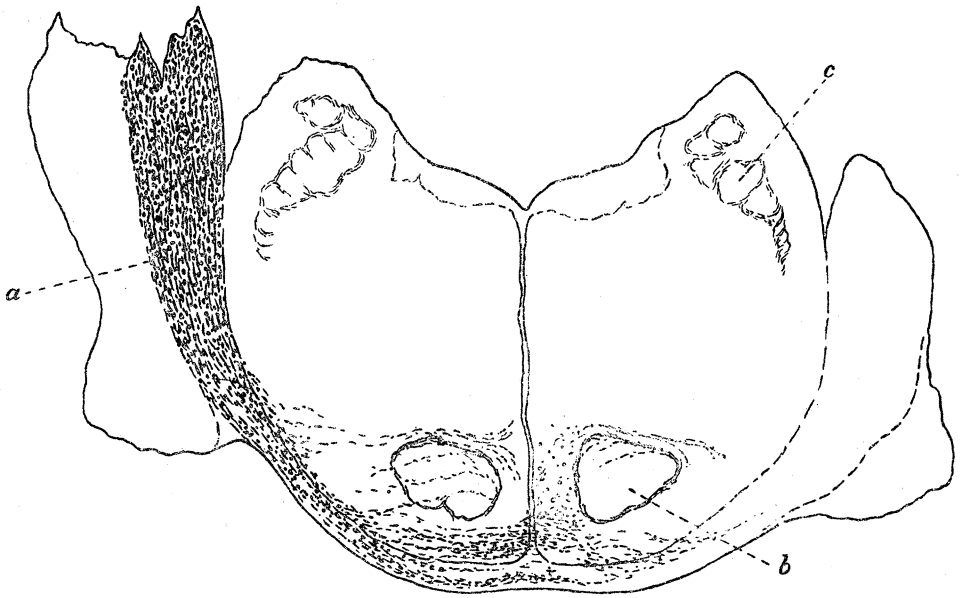
The fibres which leave the main bundle to pass on the dorsal aspect of the pyramid on the side of the cerebellar lesion, and also those which pass transversely between

Fig. 7.



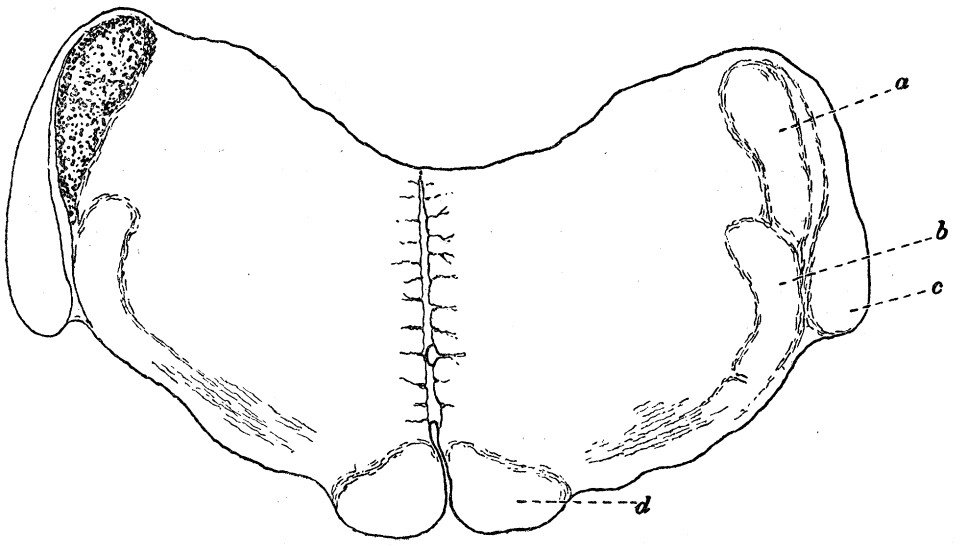
Transverse section at the upper (cephalic) end of pons, showing degeneration of the dorsal hook-like extremity of both superior cerebellar peduncles after mesial section dividing the cerebellum into two lateral halves. D and D' = degenerated fibres; a, b, c, d, e, and f as in fig. 1.

Fig. 8.



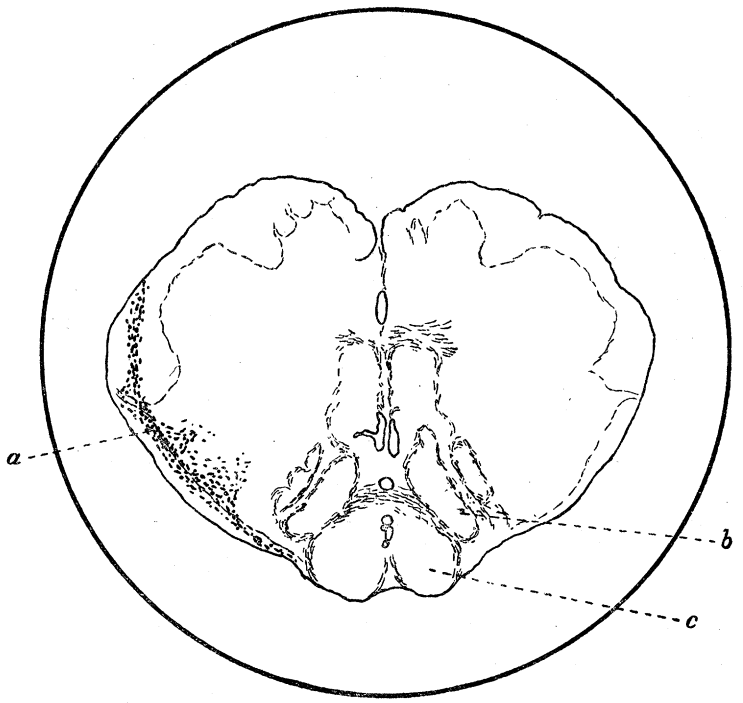
Transverse section through pons, showing degenerated fibres of the middle peduncle of the cerebellum on the same side after ablation of one lateral lobe of the organ. a = degenerated fibres of middle peduncle; b = pyramid; c = superior cerebellar peduncle.

Fig. 9.



Transverse section through upper (cephalic) end of medulla, showing degeneration limited to the restiform body on the same side after ablation of one lateral lobe of the cerebellum. a = restiform body; b = ascending root of Vth; c = root of auditory nerve; d = pyramid.

Fig. 11.



Transverse section through lower (caudal) end of medulla, showing position occupied by degenerated fibres from the inferior peduncle on the same side after ablation of one lateral lobe of the cerebellum. a = degenerated fibres of inferior peduncle; b = olive; c = pyramid.

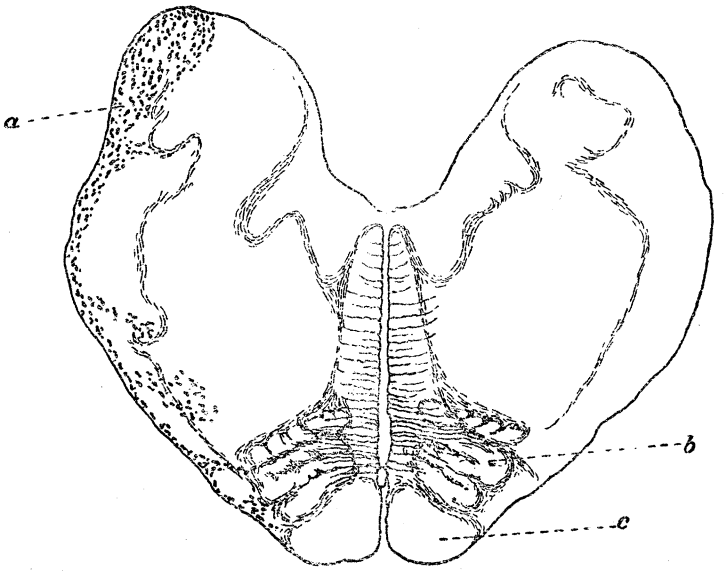
the bundles of the pyramid, do not appear to cross the raphé, and certainly the degenerated fibres which may be seen passing between the bundles of the opposite pyramid, and along its dorsal aspect, are not derived from this source but from those fibres which turn up between the raphé and the opposite pyramid, as has been already said.

The majority of the degenerated fibres of the middle peduncle terminate in the grey matter of the opposite side of the pons; but a few of these fibres terminate in the grey matter of the pons on the same side as the cerebellar lesion. No degenerated fibres from this source were traced in the fillet and posterior longitudinal bundle to the antero-lateral region of the spinal cord, or to the quadrigeminal region.

3. *The Inferior Cerebellar Peduncle.*

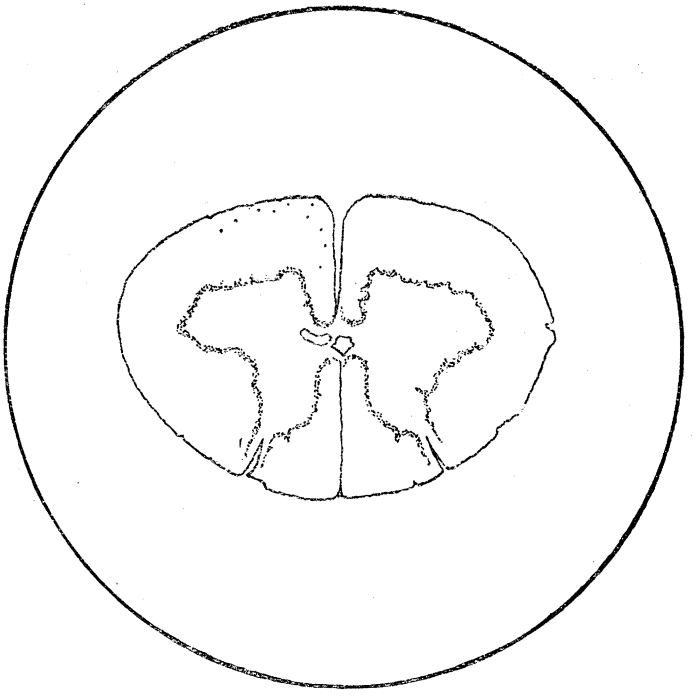
As in the case of the other peduncles, so here, the degenerated fibres at first occupy a compact region, and are not widely scattered, they are in fact accurately limited to the confines of the restiform body, on the side of the cerebellar lesion, as seen on transverse section (see fig. 9), and not a degenerated fibre is to be seen in any other region in such a section. On following these fibres in sections taken at lower levels they soon begin to show a tendency to separate from each other, and while some pursue a more or less vertical course, caudalwise, others turn into the gray matter in increasing numbers, at successively lower levels, until the few fibres left in the peripheral region of the medulla are scarcely worthy of the name of a tract. Another tendency which is evident in the degenerated fibres of the restiform body, is for them to move more or less *en masse* ventralwards, so that they come to lie more and more anteriorly, in the lateral region of the medulla, at successively lower levels. Fig. 9, taken from a section at the level of exit of the eighth cranial nerve, whose superficial root is seen coursing on the outerside of the restiform body, illustrates the accurate limitation of the degenerated fibres to the restiform body, while at a lower level the degenerated fibres still form a compact band occupying the lateral region of the medulla, external to the substantia gelatinosa Rolandi posteriorly, and the ascending root of the fifth nerve more anteriorly. But even at this level a few degenerated fibres may be seen wandering in towards the gray matter in the region of the substantia gelatinosa, and between it and the posterior part of the ascending root of the fifth nerve. The tendency for the degenerated fibres from the restiform body to move in towards the central gray matter is, however, better seen at a still lower level, as shown in fig. 10, taken from a section at the level of exit of the vagus. Here a well-marked band of degenerated fibres occupy a region internal to the ascending root of the fifth nerve, so that this root of the fifth nerve is embraced between this inner bundle of degenerated fibres and the outer band which pursues its downward course at the periphery of the lateral region of the medulla. As is seen in the figure, dorsally these two bands of degenerated fibres are

Fig. 12.



Transverse section of the medulla oblongata at about middle of inferior olive. a = degenerated fibres of inferior cerebellar peduncle; b = inferior olive; c = pyramid.

Fig. 14.



Transverse section in the cervical region of the spinal cord, showing a few degenerated fibres in the antero-lateral region on the same side after ablation of one lateral lobe of the cerebellum.

fused, and they only become separated at the posterior margin of the ascending root of the fifth nerve. Transverse sections, taken from the region of the lower end of the inferior olive (see fig. 11), show that although a well-marked tract of degenerated fibres still occupies the lateral peripheral region of the medulla, it is not so large a band as was met with at higher levels, and numerous degenerated fibres are to be seen scattered in the gray matter internal to this chief band, which occupies the region of the lateral medullary tract. Degenerated fibres pass from this peduncle to both inferior olives, but no well-marked tract of degenerated fibres, such as might have been expected, passes to the opposite inferior olive (see fig. 12). A section taken at the level of the decussation of the fillet, or superior pyramidal decussation, demonstrates the existence of degenerated fibres scattered in the gray matter on the side of the cerebellar lesion, and that near the periphery of the medulla; just external to the nucleus lateralis these degenerated fibres are more numerous, and form, in fact, a slender band (see fig. 13). This is, however, the last level at which a band of degenerated fibres, worthy of the name of a descending tract from the cerebellum, can be traced. Below this there are certainly some degenerated fibres occupying the periphery of the antero-lateral region of the cervical portion of the spinal cord, but they are extremely few, and are scattered (see fig. 14). By the time the dorsal region of the cord is reached there is scarcely a degenerated fibre to be seen, if one, occupying this antero-lateral region of the cord, in which region MARCHI figures so extensive a tract of degenerated fibres as passing down even to the lumbar region of the spinal cord, where not a single degenerated fibre was found by me after ablation of one lateral lobe of the cerebellum.

V. EXTIRPATION OF THE MIDDLE LOBE OF THE CEREBELLUM.

In removing the middle lobe of the cerebellum, in order to study the degenerations which follow such a lesion, I was always careful to avoid removing any of the lateral lobe on one or both sides. In fact, I preferred to leave a little of the middle lobe, bordering on the lateral, rather than injure the lateral lobe in my operation. In order to be still more certain that the degenerations I found were consequent on destruction of the middle lobe, and not due to any injury of the lateral lobes, I removed small portions of the middle lobe, in some cases, in which procedure there could be no possibility of the lateral lobes being injured. I therefore feel confident that the degenerations I am about to describe are due to destruction of the middle lobe, and not to any implication of the lateral lobes in the lesion.

As after ablation of one lateral lobe of the cerebellum, so here degenerated nerve fibres were found in the superior, middle, and inferior peduncles of the organ; but whereas, with the exception of the superior peduncle, degenerated fibres were only found in those of one side in the former case, they were found in all the peduncles on

both sides, after extirpation of the middle lobe, for in the case of the middle lobe the lesion was bilateral, not unilateral.

1. *The Superior Cerebellar Peduncles.*

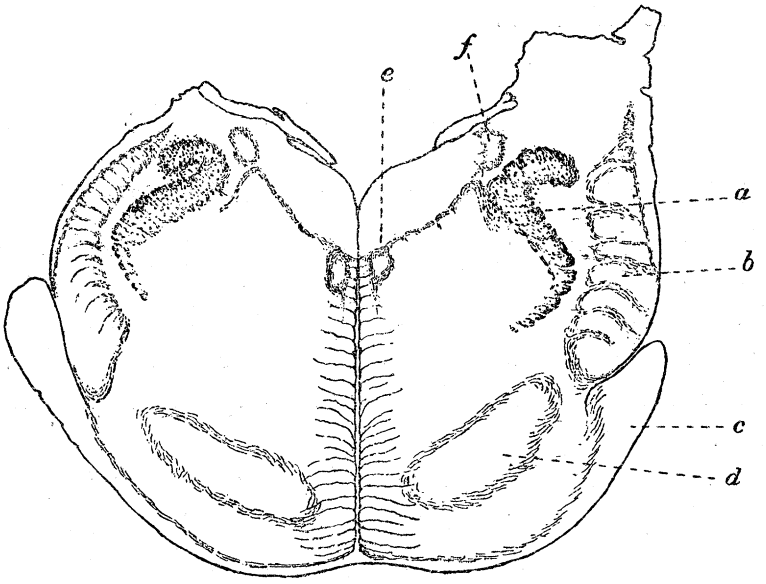
The degenerated fibres in the peduncle are scattered through all parts of it, as seen on transverse section (see fig. 15). They occupy the region occupied by those fibres which degenerate in this peduncle on the side of the lesion, after removal of one lateral lobe of the cerebellum, and also that occupied by the degenerated fibres in the superior peduncle of the opposite side, after such a lesion. So that the hook-like posterior end of the peduncle, as every other part of it, contains degenerated fibres.

On tracing these degenerated fibres upwards, they are seen to preserve the same course as those which degenerate after removal of one lateral lobe, and when the posterior quadrigeminal region is reached they decussate (see fig. 16). Owing to the degeneration being bilateral, it is difficult to be certain whether all the degenerated fibres decussate. It is, however, probable that at any rate some of those which occupy the hook-like extremity of the peduncle preserve a direct course, for they must be the commissural fibres which we found in this part of the opposite superior peduncle after ablation of one lateral lobe of the cerebellum, and in both superior peduncles when the organ was divided vertically into two lateral halves. The position occupied by the fibres which degenerate in the superior peduncle after extirpation of the middle lobe, after they have decussated, is practically the same as that occupied by those which degenerate after removal of one lateral lobe. These degenerated fibres can be traced to the red nucleus, beyond which region I have not been able to discover any degenerated fibres, after removal of the middle lobe of the cerebellum.

2. *The Middle Cerebellar Peduncles.*

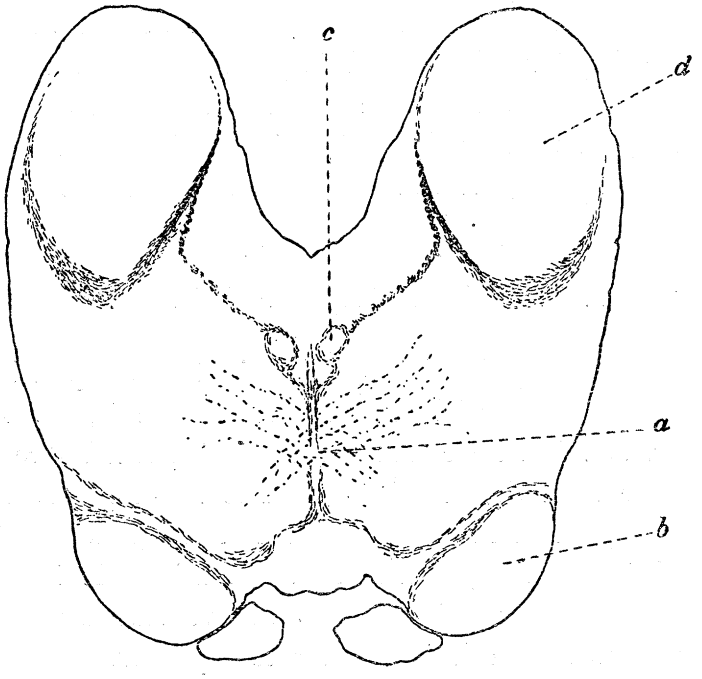
The degeneration in these peduncles though slight as compared with that which results after ablation of one lateral lobe of the cerebellum, is, nevertheless, perfectly unmistakable (see fig. 17). In their course, these degenerated fibres behave much in the same way as those from the lateral lobe. The majority pass in the superficial transverse fibres of the pons on the ventral aspect of the pyramid of their own side; but, owing to the lesion causing bilateral degenerations, it is impossible to say whether any pass across the middle line to the ventral aspect of the opposite pyramid. For the same reason it is difficult to say whether any of the degenerated fibres seen between the pyramidal bundles of one side are derived from the opposite middle peduncle or not. Degenerated fibres pass from the peduncle of the same side between the pyramidal bundles. Degenerated fibres are also to be seen

Fig. 15.



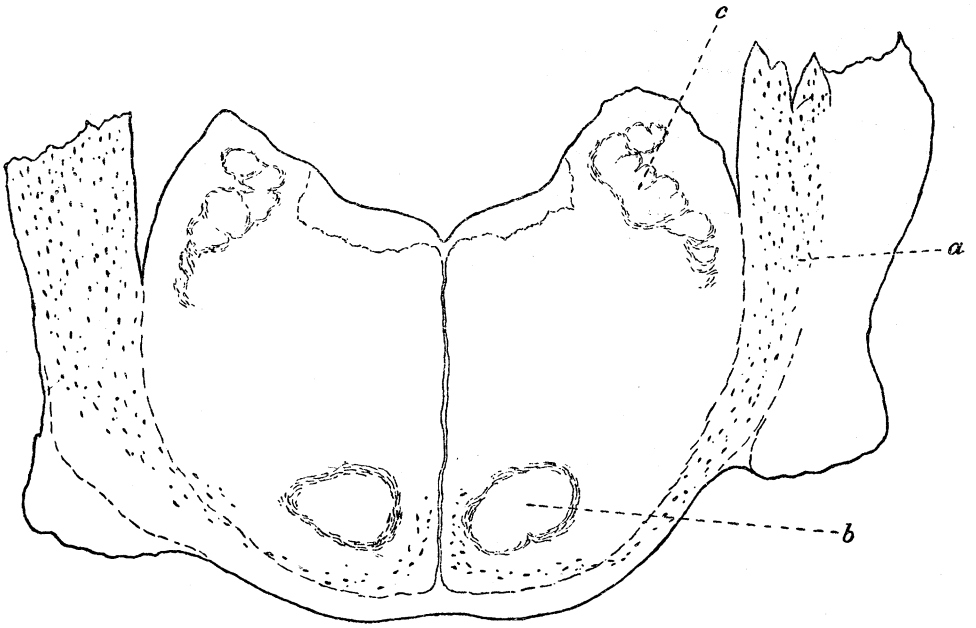
Transverse section through upper (cephalic) end of pons, showing degeneration in all parts of both superior cerebellar peduncles after extirpation of the middle lobe of the cerebellum. a = superior cerebellar peduncle; b = lemniscus; c = transverse fibres of pons; d = pyramid; e = posterior longitudinal bundle; f = descending root of Vth.

Fig. 16.



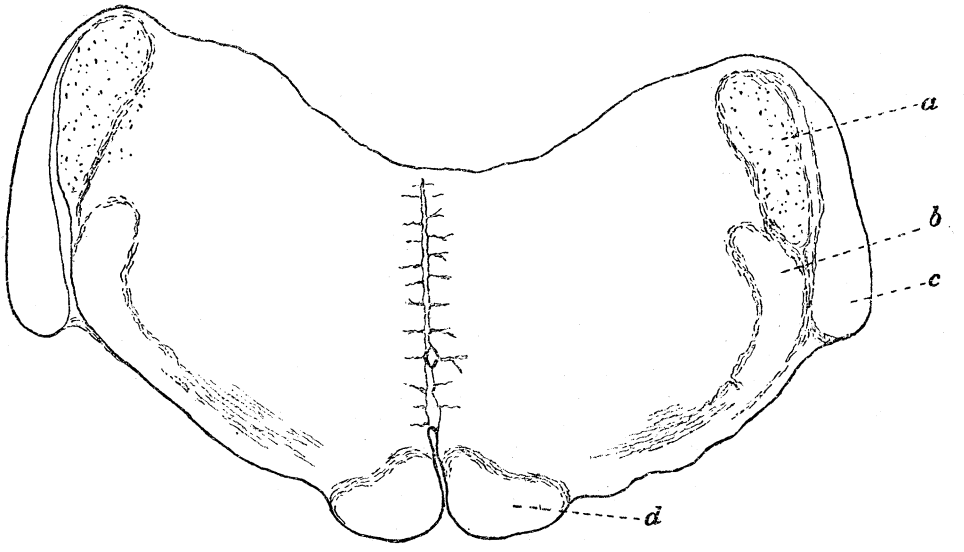
Transverse section through posterior corpora quadrigemina, showing degenerated fibres of the superior cerebellar peduncles decussating after extirpation of the middle lobe of the cerebellum. a = superior cerebellar decussation; b = pyramid; c = posterior longitudinal bundle; d = post. corp. quad.

Fig. 17.



Transverse section through pons, showing degenerated fibres of both middle peduncles of the cerebellum after extirpation of the middle lobe of the organ. a = degenerated fibres of middle peduncle; b = pyramid; c = superior peduncle.

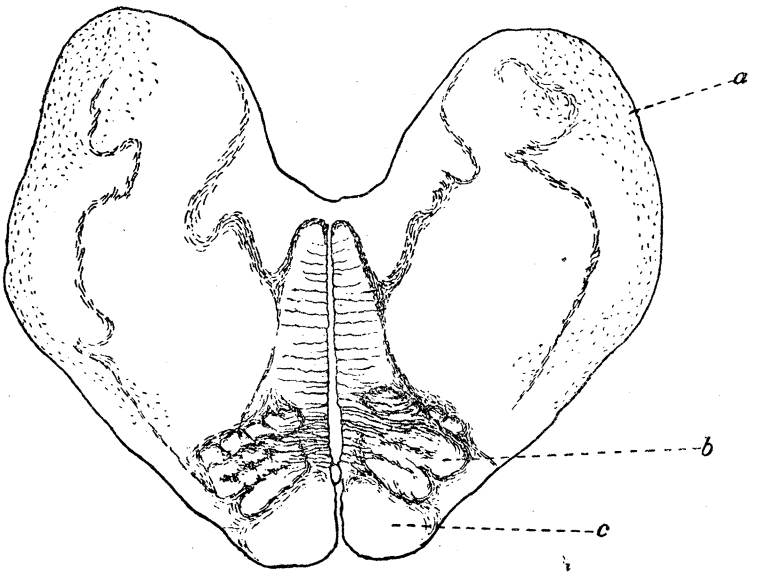
Fig. 18.



Transverse section through upper (cephalic) end of medulla, showing degeneration in both restiform bodies after extirpation of the middle lobe of the cerebellum. a = restiform body; b = ascending root of Vth; c = root of auditory nerve; d = pyramid.

between the raphé and pyramidal bundles on both sides, but owing to the degeneration in the peduncles being bilateral, it is difficult to say whether they are all derived from the middle peduncle on the same side, or from that of the opposite side. It will be remembered that after ablation of one lateral lobe the number of degenerated fibres occupying this position, between the pyramidal bundles and raphé, was much greater on the opposite side, than on the side of the degenerated middle peduncle, very few degenerated fibres appearing to pass between the pyramidal bundles and raphé on the side of the lesion.

Fig. 19.

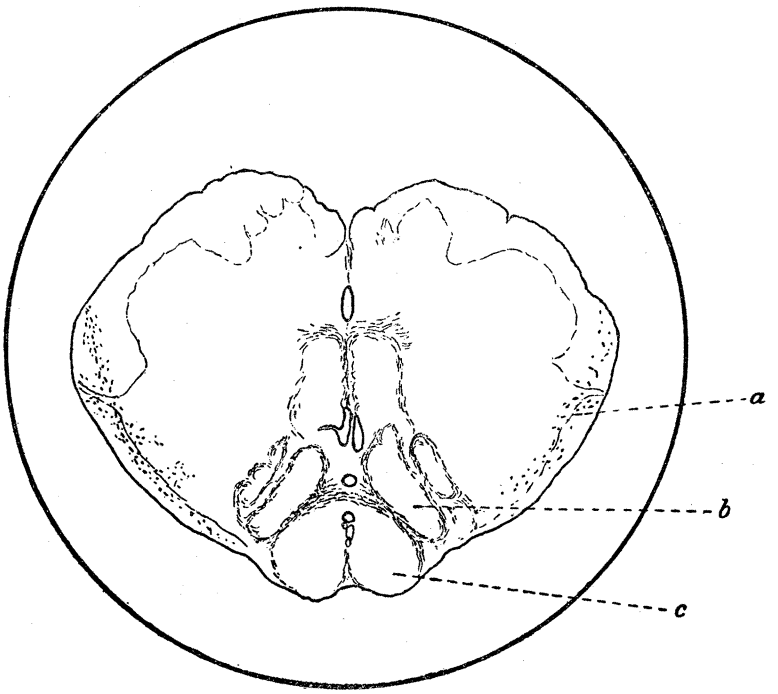


Transverse section of the medulla oblongata at about middle of inferior olive, showing degenerated fibres of inferior cerebellar peduncles after extirpation of the middle lobe of the organ. a = degenerated fibres of inferior peduncle; b = inferior olive; c = pyramid.

3. *The Inferior Cerebellar Peduncles.*

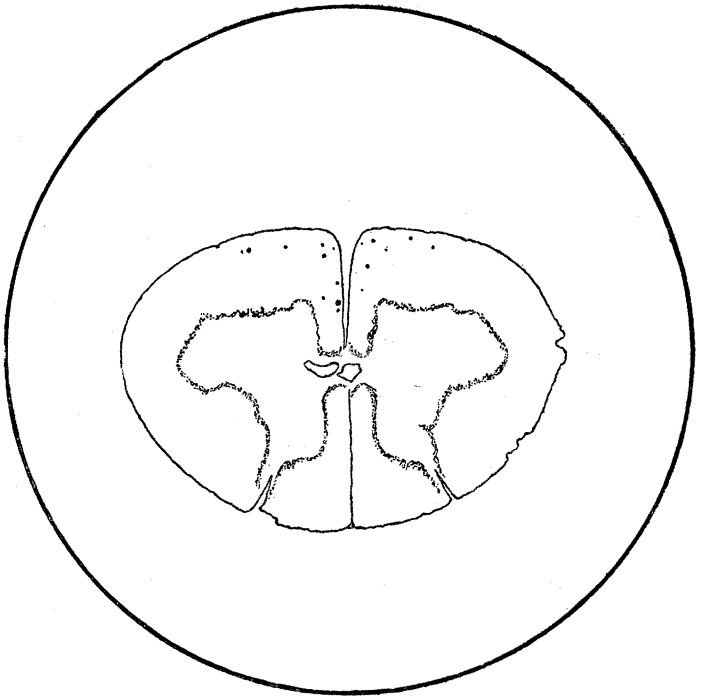
The degenerated fibres are at first limited to the confines of the restiform body, as seen on transverse section (see fig. 18). On tracing these degenerated fibres through lower levels they are seen to behave in a similar manner to those which degenerate after removal of the lateral lobe of the cerebellum, for while the bulk of the degenerated fibres occupy the periphery of the lateral region of the medulla, increasing numbers are found scattered through the formatio reticularis, as successively lower levels are reached (see figs. 19 and 20). As these degenerated fibres found in the formatio reticularis are derived from the tract which occupies the periphery of the lateral region of the medulla, this tract naturally diminishes as we pass caudalwise. To what extent the degenerated fibres in the lateral tract become scattered, may be judged from its appearance at the level of the lower portion of the inferior olive (see

Fig. 20.



Transverse section through lower (caudal) end of medulla, showing position occupied by degenerated fibres from the inferior cerebellar peduncles after extirpation of the middle lobe of the organ. *a* = degenerated fibres of inferior peduncle; *b* = olive; *c* = pyramid.

Fig. 21.



Transverse section in the cervical region of the spinal cord, showing a few degenerated fibres in the antero-lateral region on both sides after extirpation of the middle lobe of the cerebellum.

fig. 20). As after removal of the lateral lobe of the cerebellum, so here the tendency of the degenerated fibres, in the region of the lateral medullary tract, is to occupy a more and more ventral position, as successively lower levels are reached.

Of the degenerated fibres, which leave the lateral medullary tract and pass into the formatio reticularis, some can be traced to the inferior olives; but, as in the case of the lateral lobe extirpation, so here I have been unable to trace any well-marked tract of degenerated fibres to the opposite inferior olive from the lateral medullary tract of one side.

A few scattered degenerated fibres, occupying chiefly the antero-lateral region, are found in the upper part of the spinal cord (see fig. 21); but there is no evidence of a definite tract of degenerated fibres in the cord such as has been described by MARCHI. Those fibres which are found degenerated in the cord are a direct continuation of some of those which were seen to occupy the periphery of the lateral region of the medulla oblongata.

VI. SUMMARY OF RESULTS.

A. *Ablation of one Lateral Lobe of the Cerebellum.*

The paths along which degenerated nerve fibres have been traced may be summarised as follows :—

1. The superior peduncle of the side of the lesion, to the opposite red nucleus and optic thalamus chiefly, a few going to the red nucleus of the same side.

2. The superior peduncle of the opposite side; the degenerated fibres in which become intermingled with those of the other superior peduncle after it has decussated. The ultimate destination of these degenerated fibres is doubtful.

3. The fibres which degenerate in the opposite superior peduncle are true commissural fibres.

4. Degenerated fibres in the middle peduncle on the side of the lesion pass chiefly to the gray matter of the opposite half of the pons.

5. There are no degenerated fibres leaving the cerebellum by the opposite middle peduncle.

6. Those degenerated fibres, which are contained in the inferior peduncle on the side of the lesion, pass down in the region of the lateral medullary tract, and a few reach the cervical cord, where they are scattered in the antero-lateral region. The majority of the degenerated fibres, however, terminate in the gray matter of the medulla on the same side, while some pass to the opposite side. Some of these fibres pass to the inferior olive of the opposite side, and some to that of the same side.

7. No degenerated fibres are present in the opposite inferior peduncle.

8. No degeneration of the fillet, posterior longitudinal bundle, ascending root of the fifth, roots of the cranial nerves, or anterior roots of the spinal nerves was met with, nor was there a degenerated tract occupying the periphery of the antero-lateral region of the spinal cord.

B. *Extirpation of the Middle Lobe of the Cerebellum.*

1. Those fibres which degenerate in the superior peduncles decussate in the posterior quadrigeminal region, and pass to the red nucleus on the opposite side to the peduncle from which they are derived.

2. The degenerated fibres in the middle peduncles pass to the gray matter of the pons.

3. The inferior peduncles contain degenerated fibres which pass to the gray matter of the same side of the medulla, some to the opposite side, while a few scattered fibres are to be seen extending into the upper part of the spinal cord, occupying its antero-lateral region.

4. No degeneration of the fillet, posterior longitudinal bundle, cranial or spinal nerve roots was found, nor was there a degenerated tract occupying the periphery of the antero-lateral region of the spinal cord, the few degenerated fibres in the upper part of the cord being its only representatives.

VII. Comparison of Results with those recently obtained by other Observers.

On comparing the results which I have obtained with those obtained by Marchi on the one hand, and by Ferrier and Turner on the other, it is obvious that they are by no means completely in accord with those obtained by either of these observers. According to my results, all the degenerations described by Marchi do not appear to be the result of uncomplicated lesions of the cerebellum, while the degenerations which actually result from such lesions are certainly more extensive than those described by Ferrier and Turner.

It will be most convenient to consider the results obtained on ablation of one lateral lobe of the cerebellum first; but it must be remembered that while this was the operation practised by Ferrier and Turner, and in my own experiments, it was not what Luciani did. He removed one half of the cerebellum, that is, one lateral lobe, and the half of the middle lobe on the same side. Now Marchi described certain degenerations as occurring, after such an operation, which have not been met with by Ferrier and Turner, or by myself, after removal of one lateral lobe alone. It at first appeared possible that the more extensive degenerations met with by Marchi might result from the additional amount of cerebellar tissue which he removed, in the shape of half of the middle lobe; but viewed in the light of Marchi's own results when half of the middle lobe of the cerebellum was alone removed, and my own in which the whole of the middle lobe was extirpated, it is impossible to look for the explanation of the discrepancy in this direction. So that we cannot reasonably look on the destruction of the half of the middle lobe as accounting for the more extensive

degenerations met with by MARCHI. Certain of these degenerations described by him are so contrary to all our previous conceptions, based on anatomical, embryological, and experimental evidence, that it is difficult for us to avoid the conclusion that they may be the result of accidental complications, and may not represent true connections of the cerebellum. Besides the possibility of direct injury to other parts, there must have been great danger of inflammatory reaction involving adjacent parts, for more than one operation on the cerebellum was performed on the same animal, and perchloride of mercury lotion was used in the plugs inserted to stop hæmorrhage from the cerebellum. This latter procedure alone gives rise to diffuse changes which vitiate such experiments. In further support of this surmise that the degenerations in question may be accidental is the fact that, as we shall have reason to point out shortly, other observers have produced these additional degenerations by purposely injuring parts contiguous to the cerebellum, and I have myself obtained some of them by accidental injury to such parts.

With regard to the degenerations met with in the cerebellar peduncles, my own results are in accord with those of MARCHI and of FERRIER and TURNER, in so far as the middle and inferior peduncles are concerned, for I only found degenerated fibres in these peduncles on the side of the lesion, while no sign of any degenerated fibres could be detected in the middle and inferior peduncles of the opposite side. But with regard to the superior peduncles, I am compelled to join issue with these observers, for degenerated fibres are certainly to be seen in this structure on both sides after simple ablation of one lateral lobe of the cerebellum. The degenerated fibres occupy so special a position in the superior peduncle of the opposite side (see fig. 7), that it is strongly opposed to the result being an accidental one. But there is corroborative proof of the genuineness of this result in the fact that degenerated fibres occupy this position after the cerebellum has been divided into two lateral halves by a mesial incision. It thus seems clear that MARCHI'S inference that none of the cerebellar peduncles contain commissural fibres connecting the two halves of the organ is erroneous, in that the superior peduncles unquestionably appear to contain such fibres.

We are all agreed that the ultimate termination of the majority of the fibres which degenerate in the superior cerebellar peduncle on the side of the cerebellar lesion is in the opposite red nucleus and optic thalamus. MARCHI, however, describes some of these degenerated fibres as terminating in the red nucleus on the side of the lesion, while FERRIER and TURNER make no mention of having found this connection. Like MARCHI I have been able to trace degenerated fibres to the red nucleus on the side of the lesion; these are degenerated fibres of the superior peduncle which do not decussate.

That fibres of the middle peduncle, on the side of the lesion, degenerate, we are all agreed. In the abstract of their paper FERRIER and TURNER say nothing of the ultimate destination of these degenerated fibres. MARCHI, on the other hand,

describes a most extensive distribution of these fibres. That degenerated fibres from this source insinuate themselves among the pyramidal fibres of both sides, and even among the fibres of the fillet, I am ready to admit; but I am unable to confirm MARCHI'S observation that there is degeneration in the fillet and posterior longitudinal bundles up to the quadrigeminal region, and down to the periphery of the antero-lateral region of the cord. That no such ascending and descending degeneration exists in these structures, in uncomplicated lesions of the cerebellum, I feel certain. In no instance in which I have been quite certain that I have been dealing with an uncomplicated lesion of the cerebellum have I found even a suspicion of any such degeneration of the fillet or posterior longitudinal bundles.

It is obvious that there is considerable diversity of opinion among us as to the destination of the fibres which degenerate in the inferior peduncle. We have all traced degenerated fibres from this source to the opposite inferior olive it is true, but while the statements of the other observers would lead one to suppose that the degenerated fibres to the olive formed a distinct tract, my own observations do not tally with this. I have found the fibres considerably scattered in their passage to the opposite inferior olive, and not at all forming a distinct well-marked tract, such as the association of the opposite inferior olive with the lateral lobe of the cerebellum would lead one to expect. Indeed, I cannot say that I found very many more degenerated fibres passing to the opposite inferior olive than I did to that on the same side. FERRIER and TURNER'S statement would lead us to suppose that this was the chief tract which they met with from the restiform body, while I found that the chief tract continued directly downwards, or caudalwise, occupying the region of the lateral medullary tract. The absence of a satisfactory tract of nerve fibres degenerating from the cerebellum to the opposite inferior olive, in my experiments, taken in conjunction with MARCHI'S statement that a small bundle passes to this structure, makes me inclined to question whether the tract described by FERRIER and TURNER may not have been in part a secondary consequence of the atrophy of the opposite olive. In other words, whether the degenerated tract described by them is not partly an atrophied condition of that from the olive to the cerebellum, rather than a tract wholly composed of fibres degenerating from the cerebellum to the olive. Congenital defect of the opposite inferior olive, in conjunction with similar defect of one lateral lobe of the cerebellum and atrophy of the opposite olive after destruction of one lateral lobe of the cerebellum, can as readily be accounted for if we suppose the main path of connections between these structures passes from the olive to the cerebellum instead of from the cerebellum to the olive as is generally supposed. I take it that the atrophy of the olive is not consequent on any removal of a trophic influence previously exercised on it by the cells of the lateral lobe of the cerebellum that has been destroyed, but that it is an atrophy consequent on their functional relationship. Although the main tract of degenerated fibres from the inferior peduncle continues caudalwise, occupying the periphery of the lateral region of the

medulla, we have seen that I can find nothing worthy of the name of a tract lower than the level of the superior decussation, or decussation of the fillet; whereas MARCHI, of course, describes an extensive tract as degenerating in the antero-lateral region of the spinal cord down to the lumbar region. Even when making allowance for the fact that MARCHI had removed half of the middle lobe in addition to the lateral, while I had only removed the lateral lobe of the cerebellum, it is difficult to see how he could obtain so extensive a descending tract from a purely cerebellar lesion. That the descending tract described by him was a result of some accidental lesion, which complicated his operation on the cerebellum, seems possible for several reasons. Neither FERRIER and TURNER nor I have been able to detect any such tract after destruction of the cerebellum alone; FERRIER and TURNER* found a degenerated tract occupying this region of the cord after injury to DEITER'S nucleus. MOTT† found a similar tract of fibres degenerating after injury, involving the ground fibres and some of the cranial nuclei situated in the floor of the fourth ventricle, and considers it very possible that these degenerated fibres come from DEITER'S nucleus; but further suggests that they may also possibly be ground fibres from motor cranial nuclei, particularly the ocular nuclei, and serving as bridges between spinal and cranial nuclei. For these reasons then, I think we are justified in questioning the existence of a direct efferent tract from the cerebellum extending throughout the spinal cord. Further, the few degenerated fibres which do reach the cervical cord are a direct continuation of those occupying the region of the lateral medullary tract, and do not pass to the cord by way of the fillet and posterior longitudinal bundles, as stated by MARCHI. On further comparing my results with those of MARCHI, it is clear that mine are directly opposed to his when he goes on to describe degenerated fibres as passing from the restiform body to the fillet, posterior longitudinal bundle and pyramidal tract. So, too, I have not found the slightest evidence of any degeneration in the roots of the cranial and spinal nerves, or in the ascending root of the fifth, after ablation of one lateral lobe of the cerebellum; all of which negative observations are in accord with similar observations by FERRIER and TURNER.

In discussing the degenerations consequent on destruction of the middle lobe of the cerebellum, it will simplify matters if we first dispose of FERRIER and TURNER'S observations in this connection, for, as we have seen, they found no degeneration in the superior, middle, or inferior peduncles after such a lesion, while my own results confirm those of MARCHI, who found degenerated fibres in all these peduncles after a lesion of the middle lobe, unilateral after his lesion, which was unilateral, and bilateral after mine, which was bilateral. As I have said before, the fibres which degenerate after lesions of the middle lobe of the cerebellum, appear to me to be much finer than those which degenerate as a result of destruction of a lateral lobe, so that it is quite

* *Loc. cit.*

† MOTT, 'Brain,' Spring Number, 1895, and 'Proc. Physiol. Soc.,' May, 1894.

possible that such degenerated fibres may escape detection when the method chiefly relied on by FERRIER and TURNER is that employed.

Although my observations are in accord with those of MARCHI that fibres do degenerate in the superior middle and inferior peduncles of the cerebellum after lesions of its middle lobe, they by no means confirm his statements as to the course, and ultimate destination of many of these fibres.

With regard to the course and ultimate destination of the superior peduncle we are agreed. Neither of us have been able to trace any degenerated fibres beyond the opposite red nucleus, after lesions of the middle lobe of the cerebellum. Little need be said with regard to the middle peduncle, on comparing our results, but it is otherwise with regard to the inferior peduncle. As a comparison of our results shows, mine confirm MARCHI'S, in so far as he found that the degenerated fibres occupied chiefly the outer or lateral part of the restiform body, but when he goes on to state that degenerated fibres pass from this source to the cranial nerve roots by way of the posterior longitudinal bundles, and that other degenerated fibres may be traced in the fillet, I am at variance with him. I contend that no such degenerations as these result after uncomplicated destruction of the middle lobe of the cerebellum. Our results are further at variance in that MARCHI describes a tract of fibres degenerating in the antero-lateral region of the spinal cord, while a few scattered degenerated fibres in this region, in the upper part of the spinal cord, is all that I have been able to find as representing this efferent tract of his from the middle lobe of the cerebellum.

In coming to these conclusions on comparing my results with those of MARCHI it is necessary for me to make one reservation. In all my experiments I was careful to leave a thin layer of cerebellar tissue between my lesion and the pons and medulla, so as to avoid the possibility of accidental injury of these adjacent structures complicating the results of the cerebellar ablations. Further, in removing the lateral lobe I attempted to leave a small portion of it bordering on the middle lobe rather than remove part of the middle with the lateral lobe. So too, in removing the middle lobe, I attempted to leave a small part of it on either side bordering on the lateral lobes, rather than remove any of the lateral lobes with the middle. There is, therefore, just a possibility that the small portions of cerebellar tissue, which have thus escaped removal in my experiments, may be those which contain the trophic centres for the degenerated fibres which MARCHI has described, and which I have not been able to find. I do not think that this is likely, but, at the same time, such a possibility must be taken into consideration in attempting to arrive at correct conclusions.

Illustration.

The drawings have been made for me by Mr. G. T. Gwilliam, F.R.A.S., from my specimens, and are most faithful representations of the actual sections, enlarged five times. The position of the degenerated fibres in each section has also been accurately represented; but it has been necessary to exaggerate the size of the individual fibres, as their actual size as seen under so low a power of the microscope as that which was used in making the outline of the sections, is too small to allow of satisfactory reproduction.

With the exception of the four photomicrographs which are represented in the plate which accompanies this paper, all those which I made from the specimens have been preserved in the archives of the Royal Society. They illustrate all the positive points that have been shown in the drawings, and also negative points which have not been illustrated by drawings, such as the absence of degenerated fibres in the antero-lateral region of the dorsal and lumbar parts of the spinal cord after destructive lesions of the cerebellum.

Description of Plate 14.

Fig. 2. Degeneration of the superior peduncle, as seen on longitudinal section after ablation of the lateral lobe of the cerebellum on the same side in the dog. The upper left-hand corner of the photograph represents the point where the majority of these degenerated fibres are decussating.

Fig. 3. Degenerated fibres of the superior peduncle, decussating in the posterior quadrigeminal region after ablation of one lateral lobe of the cerebellum in the monkey, as seen in a transverse section in this region.

Fig. 10. Degenerated fibres of the inferior peduncle passing external and internal to the ascending root of the fifth nerve at the level of the exit of the vagus, as seen on transverse section after ablation of the lateral lobe of the cerebellum on the same side in the dog.

Fig 13 Degenerated fibres of the inferior peduncle, external to the nucleus lateralis, as seen on transverse section at the level of the decussation of the fillet, after removal of the lateral lobe of the cerebellum on the same side.

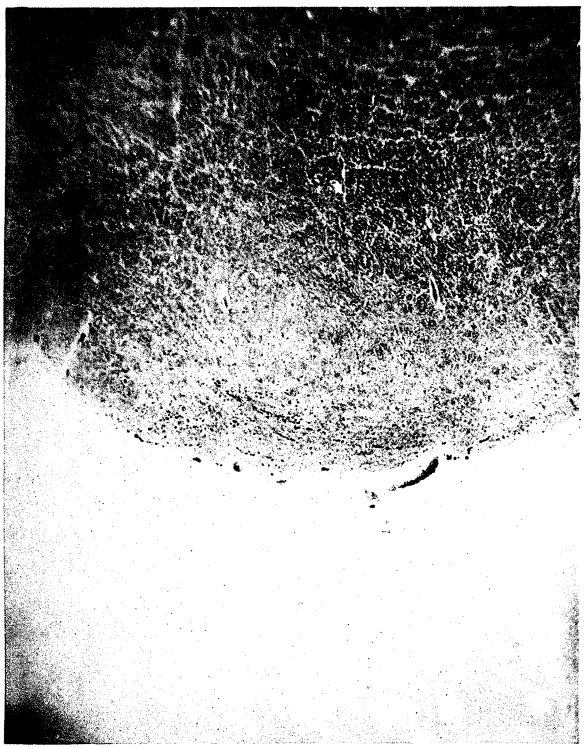


Fig. 13.

Fig. 10.

Fig. 3.

Fig. 2.

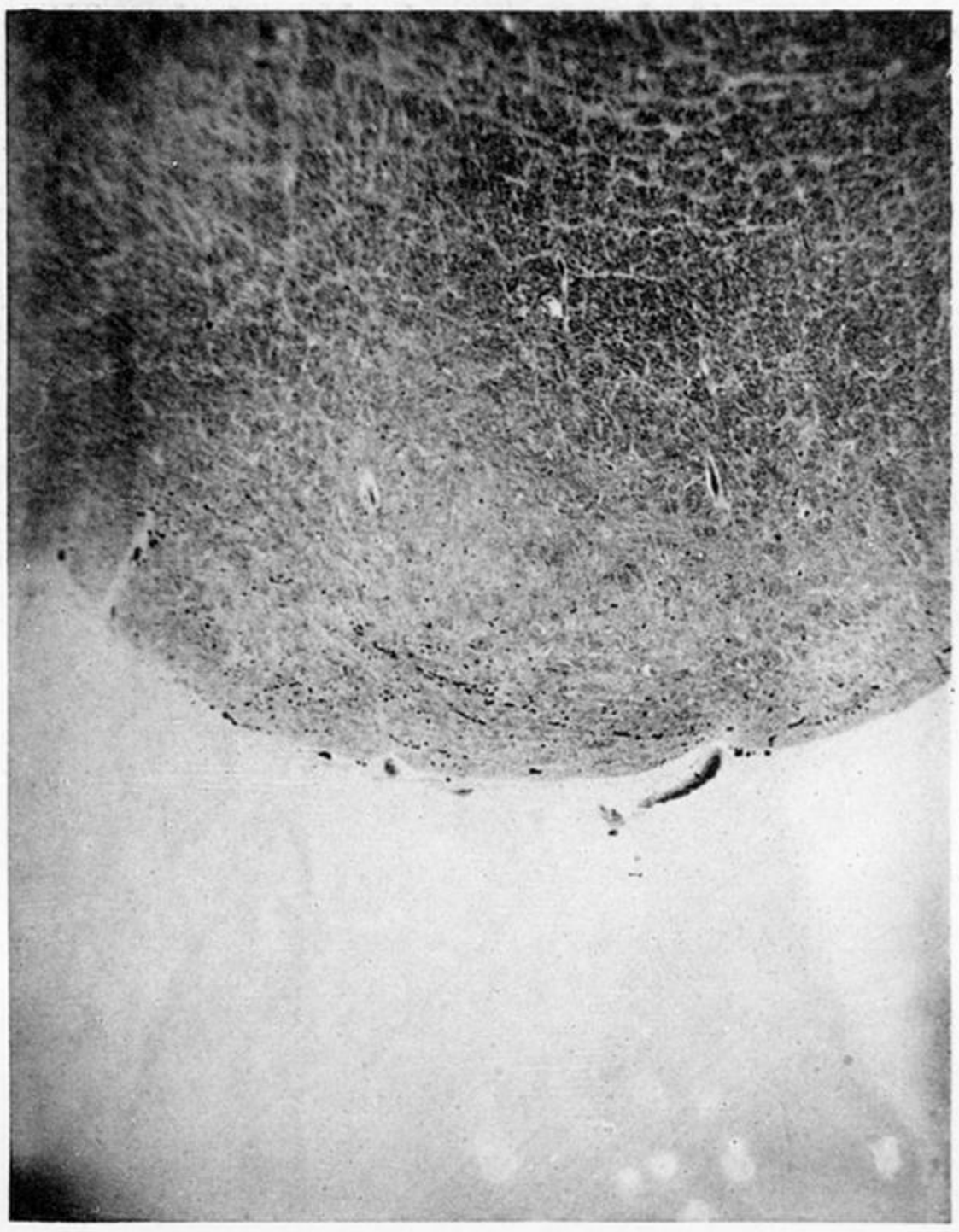


Fig. 13.

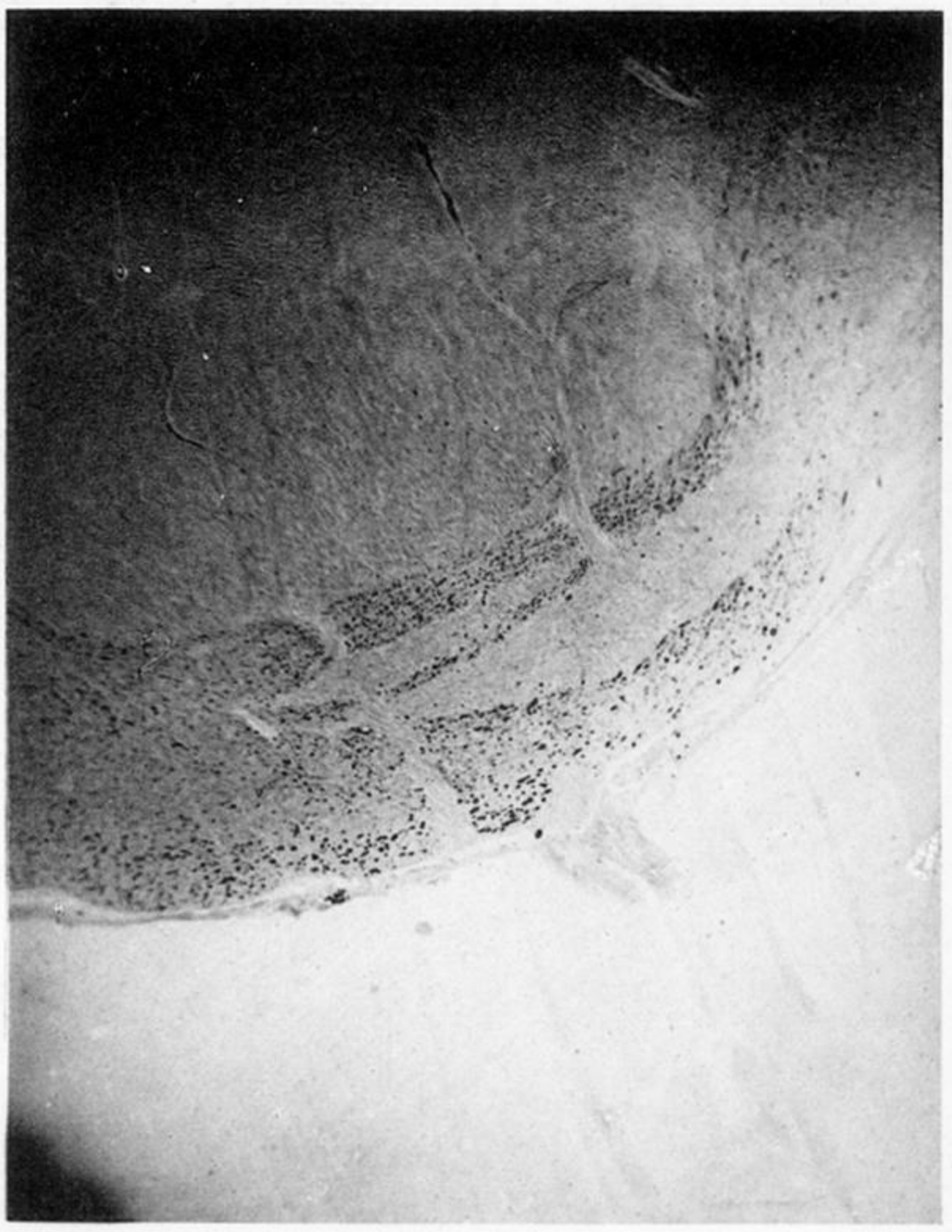


Fig. 10.

Fig. 3.

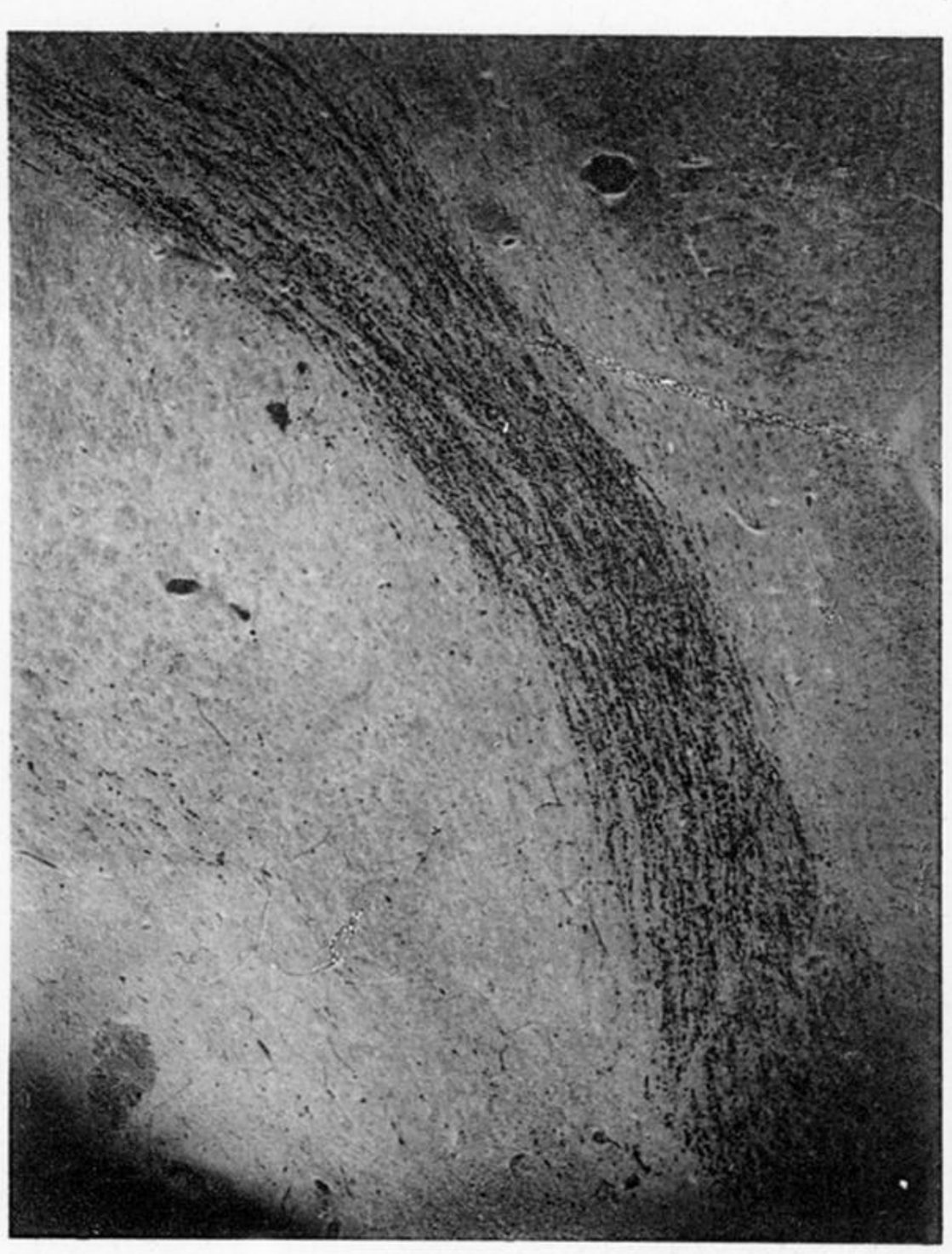


Fig. 2.

Description of Plate 14.

Fig. 2. Degeneration of the superior peduncle, as seen on longitudinal section after ablation of the lateral lobe of the cerebellum on the same side in the dog. The upper left-hand corner of the photograph represents the point where the majority of these degenerated fibres are decussating.

Fig. 3. Degenerated fibres of the superior peduncle, decussating in the posterior quadrigeminal region after ablation of one lateral lobe of the cerebellum in the monkey, as seen in a transverse section in this region.

Fig. 10. Degenerated fibres of the inferior peduncle passing external and internal to the ascending root of the fifth nerve at the level of the exit of the vagus, as seen on transverse section after ablation of the lateral lobe of the cerebellum on the same side in the dog.

Fig 13 Degenerated fibres of the inferior peduncle, external to the nucleus lateralis, as seen on transverse section at the level of the decussation of the fillet, after removal of the lateral lobe of the cerebellum on the same side.